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Effects of Telemetry Location Error on Space-Use Estimates Using a Fixed-Kernel Density Estimator

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SPACE USE AND ECOLOGY OF GOSHAWKS IN NORTHERN IDAHO

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

with a

Major in Natural Resources

in the

College of Graduate Studies

University of Idaho

By

Brian W. Moser

May 2007

Major Professor: Edward O. Garton, Ph.D.

AUTHORIZATION TO SUBMIT

DISSERTATION

This dissertation of Brian W. Moser, submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled "SPACE USE AND ECOLOGY OF GOSHAWKS IN NORTHERN IDAHO", has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Breeding habitat of northern goshawks (*Accipiter gentilis*) in North America has been associated with closed-canopy forest within the territory. I used classification trees to examine the effects of timber harvest and weather on goshawk reproduction. Classification trees showed that timber harvest did not affect goshawk nesting attempts as long as the 170-ha area surrounding the nest contained at least 39% potential nesting habitat following harvest. Increased nesting success was modeled as a function of April daily precipitation <0.3cm and January maximum daily temperature >0.7C.

Fixed-kernel density estimates using telemetry locations are used to quantify animal space use. Using simulations, I compared fixed-kernels with and without error to the true underlying distributions. The effects of telemetry error on fixed-kernels were related to sample size, distribution complexity, and ratio of median circular error probable (CEP_{0.50}) to home range size. I suggest a metric, the error ratio, to assess the adequacy of the telemetry system being used to estimate an animal's space use before a study is undertaken.

Northern goshawk space use has not been previously reported for the northern Rocky Mountain region. Mean \pm SE male and female home ranges during the breeding season using 95% fixed-kernel estimates were 5146 \pm 826 and 3859 \pm 815 ha, respectively. Mean \pm SE male and female core-use areas during the breeding season using 50% fixed-kernel estimates were 1172 \pm 210 and 762 \pm 156 ha respectively. Mean \pm SE female home ranges during the nonbreeding season were 9251 \pm 1743 ha, while core use areas were 2676 \pm 685 ha. Breeding-season home ranges were a function of nesting success and the proportions of openings and closed-canopy forest within the home range.

Resource selection studies that use samples of animal locations assume that space use is uniform. However, for central-place foragers, the null distribution is not uniform but rather a circular-normal distribution centered about the central place. I present a model for estimating a resource utilization function (RUF) that explicitly accounts for central-place foraging behavior. I demonstrate the use of bias-corrected RUFs using telemetry data from northern goshawks breeding in northern Idaho. Advantages of the bias-corrected RUF include a less-biased picture of habitat selection by central-place foragers and the ability to map goshawk habitat using the resulting model without first needing to know nest-site locations.

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TABLE OF CONTENTS

TITLE PAGE	i
AUTHORIZATION TO SUBMIT	ii
ABSTRACT	iii
ACKNOWLEDGMENTS	v
TABLE OF CONTENTS	vi
LIST OF TABLES	ix
LIST OF FIGURES	xi
CHAPTER 1: Introduction	1
Literature Cited	6
CHAPTER 2: Short-term Effects of Timber Harvest and V	Weather on Goshawk
Reproduction	9
Abstract	9
Introduction	10
Study Area	12
Methods	13
Results	
Discussion	
Discussion Management Implications	18

Literature Cited	22
CHAPTER 3: Effects of Telemetry Location Error on Space-Use Estimates	
Using a Fixed-Kernel Density Estimator	32
Abstract	32
Introduction	33
Methods	34
Results	39
Discussion	41
Management Implications	43
Acknowledgments	44
Literature Cited	44
CHAPTER 4: Estimating Northern Goshawk Space Use, Territory Fidelity,	
and Residency Status Using Satellite Telemetry	51
Abstract	51
Introduction	52
Study Area	53
Methods	54
Results	57
Discussion	60
Management Implications	63
A cknowledgments	64

Literature Cited64
CHAPTER 5: Estimating Habitat Selection: Correcting for Behavior
Associated with Central-Place Foraging72
Abstract
Introduction
Study Area77
Methods78
Results82
Discussion85
Management Implications88
Acknowledgments89
Literature Cited89
CHAPTER 6: Conclusion108
Literature Cited

LIST OF TABLES

CHAPTER 2

	Table 1. Habitat and weather variables used to develop classification tree models to
	predict goshawk territory reoccupancy and nesting success, Idaho, 2001-2004 27
	Table 2. Mean (SD) goshawk productivity, reoccupancy, and nesting success for 1
	and 2 years following timber harvest treatments, Idaho, 2001-2004
	Table 3. Mean (SD) proportion of 170-ha goshawk territories in suitable nesting
	habitat before and after timber harvest, Idaho, 2001-2004
СНАР	PTER 4
	Table 1. Mean ± SE goshawk telemetry sample sizes and space use estimates (ha)
	using 50% and 95% fixed-kernels, Idaho, 2004-2005
	Table 2. Mean ± SE goshawk 95% home range and 50% core-use area estimates for
	successful versus unsuccessful nests, Idaho, 2004-2005
	Table 3. Comparison of linear regression models used to predict goshawk home range
	size during the breeding season, Idaho, 2004-2005. Signs before variables indicate the
	relationship of each variable with home range size

CHAPTER 5

Table 1. Habitat variables associated with nest sites $(n = 14)$ from which adult
goshawks were captured and fitted with satellite transmitters for use in habitat
selection analyses, Idaho, 2004-2005.
Table 2. Explanatory variables included in regression tree analyses of goshawk
habitat selection, Idaho, 2004-2005
Table 3. Relative importance of habitat variables and relative error of regression tree
models for male goshawks, Idaho, 2004-2005
Table 4. Relative importance of habitat variables and relative error of regression tree
models for female goshawks, Idaho, 2004-2005

LIST OF FIGURES

CHAPTER 2

Figure 1. Classification tree for predicting goshawk territory reoccupancy.
Reoccupancy is predicted by the amount of potential nesting habitat remaining within
the territory after timber harvest. The mean and standard deviation amount of nesting
habitat remaining post harvest is given for the cases in each node
Figure 2. Classification tree for predicting goshawk nesting success. Nest success is
predicted by a combination of April daily precipitation and January maximum daily
temperature. The mean and standard deviation for each significant explanatory
variable is given for the cases in each node
CHAPTER 3
Figure 1. The effects of telemetry location error on volume of intersection scores for
A) 1-mode mixtures, B) 4-mode mixtures, and C) 8-mode mixtures. We did not
include standard errors in figures because they were too small to display due to the
large sample sizes
Figure 2. The effects of telemetry location error on percent relative bias for 95%
fixed-kernel contour area estimates for A) 1-mode mixtures, B) 4-mode mixtures, and
C) 8-mode mixtures. We did not include standard errors in figures because they were
too small to display due to the large sample sizes

CHAPTER 5

Figure 4. Corrected habitat selection model for male goshawks excluding distance to
nest as a potential explanatory variable. Values in each node are the mean (SD)
relative probabilities of space use associated with each decision rule
Figure 5. Corrected habitat selection model for male goshawks including distance to
nest as a potential explanatory variable. Values in each node are the mean (SD)
relative probabilities of space use associated with each decision rule
Figure 6. Uncorrected habitat selection model for female goshawks including distance
to nest as a potential explanatory variable. Values in each node are the mean (SD)
relative probabilities of space use associated with each decision rule
Figure 7. Uncorrected habitat selection model for female goshawks excluding
distance to nest as a potential explanatory variable. Values in each node are the mean
(SD) relative probabilities of space use associated with each decision rule 105
Figure 8. Corrected habitat selection model for female goshawks excluding distance
to nest as a potential explanatory variable. Values in each node are the mean (SD)
relative probabilities of space use associated with each decision rule 106
Figure 9. Corrected habitat selection model for female goshawks including distance to
nest as a potential explanatory variable. Values in each node are the mean (SD)
relative probabilities of space use associated with each decision rule

Chapter 1. Introduction

The northern goshawk (Accipiter gentilis, hereafter referred to as goshawk) has been the subject of considerable research over the past 25 years, and the subject of much litigation and controversy over the past 17 years (Squires and Kennedy 2006). Although goshawk nesting habitat was first published by Reynolds (1982), the controversy did not truly intensify until Crocker-Bedford's (1990) claim that timber harvest resulted in reduced reoccupancy and nesting success for goshawks in Arizona. This paper and a subsequent petition by environmental groups to list the goshawk as endangered west of the 100th meridian in 1991 created quite a stir among forest managers, policy makers, and biologists, particularly because these actions came on the heels of the northern spotted owl (Strix occidentalis caurina) listing as a threatened species in Pacific Northwest forests. The social and economic impacts of reduced timber harvests due to the spotted owl listing was just beginning to be felt on both public and private forest lands (Carroll 1995), and many felt that the listing of the goshawk under the Endangered Species Act could have far wider consequences due to the goshawk's wide distribution across the western United States (Squires and Reynolds 1997). From 1990 to 2005 over 30 legal or administrative actions were taken by the courts and federal agencies related to the management and legal status of the northern goshawk (Squires and Kennedy 2006). During that same time period the average number of peer-reviewed studies published per year on the goshawk in North America nearly tripled from the previous 15 years (B.W. Moser, unpublished data). It appears that one of the fortuitous consequences of the petition to list the goshawk as an endangered species was an increased interest in

goshawk research, resulting in a greater understanding of the biology and ecology of the species in North America.

Although much research has been conducted on goshawk ecology, a number of information gaps still exist, particularly regarding the effects of forest management on goshawk nesting ecology (Squires and Kennedy 2006). As Squires and Kennedy (2006) point out, the paucity of experiments testing the effects of timber harvest on goshawk reproduction is perplexing considering the common assertion from the many authors of correlative studies that goshawks may be sensitive to timber harvest within nesting territories. Many authors have demonstrated a positive correlation between closed-canopy, mature forest structure within the territory and goshawk reproduction (see review by Greenwald et al. 2005). However, only 3 authors have studied the effects of timber harvest on goshawks in North America in a quasi-experimental framework (Crocker-Bedford 1990, Mahan and Doyle 2005, Patla 2005). This is significant because the power to infer cause and effect is much stronger in a quasi-experiment than a correlative study (Garton et al. 2005). The conclusions of these 3 studies were mixed, with 2 finding a negative effect of timber harvest on goshawk reproduction (Crocker-Bedford 1990, Patla 2005) and 1 finding no effect (Mahon and Doyle 2005). Different study areas, methods, and results have undoubtedly affected our ability to distill the results of these 3 studies down to a definitive working hypothesis on the effects of timber harvest on goshawk reproduction. Although it is apparent from 2 of these studies and the many correlative studies that goshawks need some minimum amount of suitable nesting habitat in order to successfully reproduce (Squires and Reynolds 1997), what is not apparent is how much is necessary and what happens when this habitat is reduced by timber harvesting.

I attempted to address the above question in Chapter 2 by setting up a quasi-experimental, before-after/control-impact study design in a managed forest landscape in northern Idaho. Twenty-one goshawk nesting territories were monitored before and after clearcutting treatments through the nesting area, with 10 of these territories used as controls. Preliminary data on reproductive success within these territories indicated temporal variation not related to timber harvesting. Thus I decided to include the effects of winter and spring weather in my models of goshawk reproduction because other researchers have demonstrated a correlation between weather and goshawk reproduction in other areas of North America (Fairhurst and Bechard 2005). Although the sample sizes for this study were relatively small and the study duration relatively short, the results nevertheless provide data on the interactions of habitat and weather on goshawk reproduction in this region.

Goshawk space use for most North American populations is another area of goshawk ecology that is not well understood, because relatively few telemetry studies have been conducted on goshawks. Breeding-season home ranges for adult goshawks may be the exception, but we still have limited or no data for many populations, including northern Idaho. Only a handful of researchers have studied winter space use of goshawks (Squires and Ruggiero 1995, Drennan and Beier 2003, Boal et al. 2003, Sonsthagen et al. 2006). We know very little about goshawk winter home ranges, habitat use, and migratory behavior in North America. Furthermore, most of what we know about goshawk habitat comes from studies that have examined habitat in various-sized circles around nest sites (McGrath et al. 2003). Although these studies have increased our knowledge of habitat conditions in circles around goshawk nest sites relative to random circles, they have failed to address 3rd order habitat selection, which is selection for habitats within the home range (Johnson 1980). Although

those home ranges are unknown, they are much less informative than studies that examine actual habitat use within real goshawk home-range boundaries. The only published goshawk habitat study in northern Idaho was conducted by Hayward and Escano (1989) who reported habitat characteristics at the 0.04-ha scale around nest trees. Lastly, all of the researchers that have reported on breeding-season habitat selection based on radio telemetry have failed to take into account the effects of central-place foraging behavior on their habitat selection models (Rosenberg and McKelvey 1999). Failure to account for the behavior of repeatedly returning to a central place such as a nest site will bias space-use estimates to areas near the nest site. Failure to correct for central-place foraging behavior results in habitat-selection models that inaccurately depict habitat around nest sites as important for foraging and other activities (Rosenberg and McKelvey 1999), when in fact it may not be important foraging habitat for goshawks.

I attempted to address some of the above information gaps in Chapters 3-5. In Chapter 3 I tackled the feasibility of using satellite telemetry to study goshawk space use. Satellite telemetry using platform transmitter terminals and Argos satellites has been a historically inaccurate telemetry system, particularly for small transmitters designed for use on birds (Keating et al. 1999). I wanted to understand how various levels of radio-telemetry error affected space-use estimates using a fixed-kernel density estimator so I simulated various levels of telemetry error and assessed the effects on fixed-kernel space-use estimates. I developed a metric, the error ratio, which allows one to assess the effects of telemetry error before a study is undertaken to determine the size of telemetry error effects on space-use estimates.

The results of Chapter 3 indicated satellite telemetry could be used to assess space use in a wide-ranging bird such as the northern goshawk. Therefore, I proceeded to use satellite telemetry to assess male and female goshawk space use, including home range size, core-use areas, residency status, and territory fidelity in Chapter 4. No studies have been published on goshawk space use in the northern Rocky Mountain region. In this chapter I provide the first estimates of breeding-season home ranges for male and female goshawks. Furthermore, I provide home range estimates for wintering female goshawks, as well as their residency status and territory fidelity. Lastly, I developed models that linked home range sizes during the breeding season with nesting success and proportion of the home range in openings and closed-canopy forests.

In Chapter 5 I attempted to model goshawk habitat selection during the breeding season while accounting for behavior associated with goshawk central-place foraging. I extended the method of relating utilization distributions to resources (Marzluff et al. 2004, Millspaugh et al. 2006) by creating a corrected utilization distribution that attempted to remove the effect of central-place foraging from the utilization distribution before the habitat-selection models were built. The results of this chapter demonstrate the consequences of not accounting for central-place foraging behavior in habitat-selection models, as well as provide insight into physical habitat features such as elevation and distance to streams that may be important to goshawks.

My goal for this dissertation was to provide forest managers and biologists with information that would allow them to manage habitats in a manner that ensures the sustainability of goshawk populations in this region. Although my research did not address population viability per se, I believe it provided at least some of the information necessary to

concurrently manage forests for timber production while providing for the ecological needs of goshawks that both breed and winter in the forests of northern Idaho.

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Chapter 2. Short-term Effects of Timber Harvest and Weather on Goshawk Reproduction

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ABSTRACT The nesting habitat of the northern goshawk (*Accipiter gentilis*) in North America has been associated with the amount of mature, closed-canopy forest within the nesting area. However, few studies have experimentally tested the effects of timber harvest on goshawk reproduction. We studied the effects of clearcutting within the 170-ha nesting territory on reoccupancy and nesting success for 2 years following disturbance. We also examined the effects of winter and spring weather on goshawk reoccupancy and nesting success. We used classification trees to relate goshawk reproduction to habitat and weather variables. Classification trees showed that timber harvest did not affect goshawk territory reoccupancy as long as the 170-ha area surrounding the nest contained >39% potential nesting habitat following harvest. However mean (SD) proportion of habitat remaining in reoccupied territories was 0.57 (0.16) in year 1, and 0.58 (0.19) in year 2. Increased nesting success was related to mean April daily precipitation <0.3cm and mean January maximum daily temperature >0.7C. In the short term, goshawks are more likely to attempt nesting in territories after disturbance if >39% of their territory is left in potential nesting habitat.

However, our models suggest that once goshawks attempt nesting, nesting success is more likely to be a function of winter and spring weather.

KEY WORDS *Accipiter gentilis*, CART, classification tree, modeling, nesting success, northern goshawk, reproduction, timber harvest, weather.

Crocker-Bedford (1990) was the first to report adverse effects of timber harvest on northern goshawk (*Accipiter gentilis*) territory reoccupancy and reproductive success in North America. Since 1990, numerous researchers have demonstrated a positive correlation between goshawk reproduction and quantity of suitable habitat at various scales (see review by Andersen et al. 2005). Most of these studies have been observational, thus limiting the strength of their inference (Garton et al. 2005). Only 2 published studies other than Crocker-Bedford (1990) have incorporated a replicated before-after/control-impact (BACI) design to test the effects of timber harvest on North American goshawk reproduction (Mahon and Doyle 2005, Patla 2005). This is significant, because a replicated BACI study design has more power to infer cause and effect than an observational study (Garton et al. 2005). Mahon and Doyle (2005) reported no significant adverse effects of timber harvest on territory reoccupancy or nesting success in British Columbia, while Patla (2005) reported reduced territory reoccupancy and nesting success due to timber harvest in southeast Idaho.

European studies incorporating replicated BACI designs have demonstrated minimal short-term effects of habitat loss on goshawk territory reoccupancy and nesting success (Penteriani and Faivre 2001, Penteriani et al. 2002). Timber harvest within goshawk nest stands in Italy and France did not affect goshawk reproduction until the original canopy cover was altered by >30% (Penteriani and Faivre 2001). Likewise, windthrow resulting in

<30% loss of canopy cover within nest stands resulted in no measurable short-term effect on goshawk reproduction in France (Penteriani et al. 2002).

In addition to habitat loss, other factors such as weather may influence goshawk reproduction. McClaren et al. (2002) hypothesized that temporal patterns such as weather and prey availability influenced goshawk reproduction more than spatial patterns such as habitat characteristics. Weather can potentially affect goshawk reproduction through many mechanisms, including adult, egg, and nestling mortality, prey density and availability, and hunting success. However, few researchers have examined the effects of weather on goshawk reproduction. Fairhurst and Bechard (2005) found that winter and spring weather variables contributed significantly to goshawk reproduction over a 10-yr period in Nevada.

Conversely, Patla (2005) found no significant contribution of weather variables to goshawk reproduction. In Europe, researchers have reported increased precipitation and decreased winter and spring temperatures negatively affect goshawk reproduction. (Marquiss and Newton 1982, Kostrzewa and Kostrzewa 1991, Kruger and Lindstrom 2001).

Goshawk management in North America continues to be controversial (Andersen et al. 2005), partially due to contradictory study results, observational studies with weak inference, and narrowly-focused studies not incorporating multiple factors potentially affecting goshawk reproduction. Few studies have examined the effects of both habitat and weather variables on goshawk reproduction. Although Patla (2005) found no effect of weather, Kruger and Lindstrom (2001) found that models incorporating both habitat and weather best explained goshawk reproductive success in Germany.

The objectives of this study were to determine what factors affect goshawk reproduction in managed forests of northern Idaho. Specifically, do timber harvest, weather,

or a combination of these 2 factors affect goshawk territory reoccupancy and nesting success?

STUDY AREA

Our study took place within an 890,000-ha region of the Clearwater Mountains in northern Idaho, bounded in the south by the Middle Fork Clearwater River and in the north by the St. Joe River. Elevations ranged from 750-1500 m and annual precipitation ranged from 75-125 cm. Forests in this region are managed primarily for timber production, and the 3 primary landowners were Potlatch Forest Holdings, Inc., Idaho Department of Lands, and the U.S. Forest Service (Clearwater National Forest and Idaho Panhandle National Forest). Although forest types ranged from dry ponderosa pine (*Pinus ponderosa*) to cold subalpine fir (Abies lasiocarpa) habitat types, over 85% of the landscape consisted of mesic western redcedar (Thuja plicata) and western hemlock (Tsuga heterophylla) habitat types (Cooper et al. 1991). This landscape has a history of both natural and anthropogenic disturbance. Prior to European settlement, large stand-replacing fires occurred on the order of every 150-400 years within the western redcedar and western hemlock habitat types (Smith and Fischer 1997). Although fire suppression has reduced the frequency and extent of fires more recently, these lands are highly productive and intensive timber harvest has occurred in the region for the past 100 years. These disturbances have resulted in a heterogeneous forest structure, including early to late-seral stands.

Goshawk nesting habitat in our study area has been described by Hayward and Escano (1989). Goshawks usually nest in stick platforms built against the bole of live conifers below the canopy. Mean nest tree height is 31 m and dbh is 58 cm. Goshawks nest in closed-canopy (75-85% overstory cover) conifer forests on moderate slopes. Goshawk nest

stands have a mean basal area of 40 m^2 per ha. Highest tree densities per ha are comprised of the 7.6 to 17.8 cm dbh class (mean = 475), followed by the 17.8 to 30.4 cm dbh class (mean = 265), 30.4 to 60.9 cm dbh class (mean = 175), and trees >60.9 cm dbh (mean = 20).

METHODS

Nest Area Surveys

Carroll et al. (2006) recently studied 565 goshawk nest locations and found that goshawk nest-site occurrence was best predicted using habitat variables in 170-ha area around the nest. This area has been referred to as the post-fledging area due to its use by young goshawks soon after fledging (Kennedy et al. 1994). It may also correlate to the defended portion of a goshawk's territory (Reynolds et al. 1992). Thus, we used the 170-ha territory as our unit of analysis, which we defined as the 170-ha circle centered on 1 or more known nests used by breeding goshawks. Goshawk territories (n = 21) were initially located both opportunistically (n = 16) and through dawn and call playback surveys (n = 5) from 2001-2003. All territories included in the study were occupied and successfully fledged young the first year, and we monitored them for reoccupancy and nest success during each of the following 2 years. Each territory was visited a minimum of 3 times in each subsequent year, once during the courtship (10 Mar-10 Apr) or incubation period (10 April-10 May), once during the nestling period (10 May-20 Jun), and once during the post-fledging period (20 Jun-15 Aug). This level of sampling was necessary to achieve a high-detection rate (Boyce et al. 2005). We conducted predawn surveys during the courtship period (Penteriani 1999), while stand searches (Boyce et al. 2005) and call-playback surveys (Kennedy and Stahlecker 1993) were conducted during the incubation through fledging periods. We considered territories reoccupied when at least 1 adult was observed near a stick nest during

the nesting period (March 15-June 30), and when at least 1 of the following conditions occurred: 1) a goshawk was observed incubating or brooding on a nest, 2) eggs or young were observed in a nest, 3) molted feathers were found within 50 m of a nest, 4) a nest contained green twigs and downy feathers. We monitored reoccupied territories weekly to determine the fate of the nestlings. We considered territories successful if at least 1 nestling was observed in a nest within 1 week of fledging, or if fledglings were observed in the territory after June 15. We defined productivity as the number of young fledged per nesting attempt in a given year.

Harvest Treatments

All forest stands containing nests were in vegetation structural stages 4, 5, or 6, meaning they had a minimum of 70% overstory tree canopy closure and an overstory tree dbh of >31cm (Reynolds et al. 1992). We chose nest stands for harvest (n = 11) based primarily on logistical constraints such as existing harvest contracts. All harvested stands were clearcut, with 85-95% of tree volume removed from the stand and remaining trees distributed primarily in a randomly dispersed fashion. In some cases small groups of trees were retained. However none of the remaining groups were ever nested in again. Mean (SD) clearcut size was 42 (21) ha. Timber harvest occurred within the nesting stand, which was defined as the area with an occupied goshawk nest the previous year. In some cases 1 or more nest trees were removed from the stand. However, because goshawks have 3-8 nest trees a maximum of 0.8 km apart that they alternate among years (Woodbridge and Detrich 1994) it is unlikely that we removed all of the nest trees. In all cases the nest stand was altered in such as way that it no longer was expected to contain suitable nesting habitat around the previous years' nest. However, all of the nest areas had suitable habitat remaining

adjacent to the harvest unit. All timber harvest occurred after the nesting season once the adults and fledglings had left the nest stand. Timber harvest was conducted during 2001 (n = 1), 2002 (n = 3), and 2003 (n = 7). We began monitoring of a similar number of control stands in each year: 2001 (n = 2), 2002 (n = 3), and 2003 (n = 5).

Weather Variables

We collected weather data for each nesting area from the closest weather station that was at or near the same elevation as the nest area. Data were downloaded from the National Weather Service at http://www.insideidaho.org/asp/liststations.asp for the years 2001-2005. The weather variables we chose included daily mean precipitation and daily mean maximum temp for each month from Jan through May (Table 1). We chose precipitation and temp because they have been shown by other researchers to be important factors affecting goshawk reproduction (e.g., Fairhurst and Bechard 2005). This time period represents the time directly preceding the breeding season into the nestling-rearing stage, which is when goshawk reproduction is likely to be most affected by extreme precipitation and temperatures.

Data Analyses

We mapped goshawk nests in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California) and placed a 170-ha circle around each nest found in year 0, the year before any timber harvest was conducted. We delineated potential nesting habitat within each nest area using 2002 Landsat 7 satellite imagery to define cover types. Potential nesting habitat was defined as forest with >70% overstory tree canopy closure containing dominant and subdominant trees at least 31-46 cm DBH. This classification corresponds with Reynolds et al. (1992) vegetation structural stages 4-6. We ground-truthed all nest areas to

determine cover-type classification accuracy by systematically placing 48 plots in a 30-ha circle around nests and measuring trees per ha on variable radius plots using a 20-BAF factor and a densiometer to measure overstory tree canopy closure. Classification accuracy of Landsat 7 satellite imagery for potential nesting habitat was 91%.

We treated nest-area reoccupancy and nesting success as binary outcomes, and computed mean (SD) number of young fledged for each of 2 years following timber harvest. We also computed mean (SD) distance moved between nests from the year prior to harvest to the first year after harvest. We modeled territory reoccupancy and nesting success as a function of habitat and weather variables (Table 1). Data from the 21 goshawk territories were pooled across 2 years for a total of 42 cases used for modeling. A variable was included in the models to account for variation associated with time since harvest.

We used classification trees using CART 5.0 (Salford Systems, San Diego, California) to model goshawk-territory reoccupancy and nesting success. Classification trees are a non-parametric modeling technique used to explain the variation of a single response variable using 1 or more explanatory variables (Breiman et al. 1984). The main purpose of a classification tree is to produce a tree-structured predictor to explain the relationships that exist between the response and explanatory variables and to predict the response variable from new values of the explanatory variables. Classification trees identify complex hierarchical relationships in multivariate data by repeatedly splitting the data into increasingly smaller subsets in an attempt to minimize the variance in each subset. The model is initially over fit and then pruned using ν -fold cross-validation to select the most parsimonious model that maximizes classification accuracy while simultaneously minimizing

model complexity (Breiman et al. 1984). Classification trees have been used in numerous ecological studies and often outperform linear models (De'ath and Fabricius 2000).

We developed multiple models for each response variable. Model fit was evaluated based on correct classification rates using 10-fold cross-validation on the original data. We chose the best model based on cross-validation classification accuracy. We report only the best model for each response variable.

RESULTS

We monitored 21 goshawk territories during the study for 1 year preharvest and 2 years postharvest. We found no differences in territory reoccupancy, nesting success, or productivity between harvested and non-harvested areas in year 1 or year 2 following treatment (Table 2). Mean (SD) distance moved from nests in year 1 to year 2 were 155 (150) m in harvested and 100 (83) m in unharvested territories. The mean amount of potential nesting habitat remaining after timber harvest was higher for reoccupied versus unoccupied territories (Table 3). However the variance about the means was high, suggesting no statistically significant differences or sample sizes too small to detect differences. Mean potential nesting habitat remaining after timber harvest was similar for successful versus unsuccessful nests (Table 3).

The territory reoccupancy model included only amount of potential nesting habitat postharvest as a significant predictor (Fig. 1). The classification tree predicted a goshawk territory to be reoccupied when the 170-ha territory contained >39% potential nesting habitat. Correct classification rates for both the learning and cross-validated data were 89% for reoccupied territories and 63% for unoccupied territories with an overall correct classification rate of 83%.

The nesting success model was more complex than the reoccupancy model and included Apr mean daily precipitation and Jan mean maximum daily temp, in that order of importance (Fig. 2). The model predicted goshawk nests to be unsuccessful if: 1) Apr mean daily precipitation was >0.3 cm or 2) Apr mean daily precipitation was <0.3 cm and Jan maximum daily temp was <0.7 C. The model predicted a successful nest if Apr mean daily precipitation was <0.3 cm and Jan maximum daily temp was >0.7 C. The model fit the learning data with a correct classification of 75% for unsuccessful nests and 78% for successful nests with an overall correct classification rate of 76%. The cross-validated model correctly classified 67% of successful nests and 63% of unsuccessful nests with an overall correct classification rate of 64%.

DISCUSSION

Timber harvest activity within the nest area did not appear to have a large effect on goshawk territory reoccupancy until the amount of potential nesting habitat remaining in the nesting territory fell below 39%. However, nesting success was a function of winter and spring weather. With regards to timber harvest and goshawk reproduction our findings are similar to those of Mahon and Doyle (2005) in British Columbia, and studies in Italy and France (Penteriani and Faivre 2001, Penteriani et al. 2002), all of which found that habitat modification within goshawk nest areas did not adversely affect goshawk territory reoccupancy or nesting success. Our findings contradict those of Crocker-Bedford (1990) and Patla (2005) who found that goshawk territories subjected to some type of timber harvest exhibited lower reoccupancy and nest-success rates. However, Crocker-Bedford (1990) studied the effects of extensive timber harvest treatments (>1000 ha) on goshawk reproduction. Although our study involved more intensive timber harvest, it was in a much

smaller area than Crocker-Bedford (1990). The differences in timber harvest treatments may also be responsible for the differences in our results. The timber harvest treatments in Crocker-Bedford's (1990) study were conducted across large areas (1000-5000 ha), which may be more likely to negatively affect goshawk reproduction by affecting the quality of foraging habitat. Subsequent unpublished analyses suggested timber harvest within goshawk nesting areas had adverse effects on goshawk reproduction (C. Crocker-Bedford, personal communication).

Although the classification tree suggested a threshold of 39% for potential nesting habitat within the nesting territory, the mean amount of potential habitat remaining was actually around 57-58% for reoccupied territories, indicating goshawks may prefer to reoccupy territories with higher amounts of nesting habitat than suggested by the classification tree.

Our findings that winter and spring weather affected goshawk reproduction are similar to those of Fairhurst and Bechard (2005) in Nevada, Keane et al. (2006) in California, and Europe (Marquiss and Newton 1982, Kostrzewa and Kostrzewa 1991, Kruger and Lindstrom 2001). In addition, McClaren et al. (2002) suggested temporal patterns such as weather and prey availability may have influenced goshawk reproduction more than spatial patterns such as habitat characteristics. Our findings contradict those of Patla (2005) who found no effects of weather on goshawk reproduction. However, her study examined the effects of drought rather than cold, wet winter and spring weather.

It is clear from the large number of studies examining goshawk nesting habitat that goshawks prefer to nest in relatively closed-canopy forests, and that they generally select larger stands of this cover type when available (Andersen et al. 2005). What is not

conclusive, however, is how sensitive goshawks are to habitat modification within their nesting area or territory. Habitat modification could potentially affect goshawks in a variety of ways, including direct disturbance effects during nesting, and secondary effects from exposure to weather and aerial predators, increased competition from open habitat species, and changes in prey availability. Most habitat modification studies have been implemented outside of the nesting season, which rules out direct disturbance effects. Of interest is the apparent discrepancy between studies in higher productivity forests (e.g., northern Idaho, British Columbia, France, and Italy) and those in lower productivity forests (e.g., southeastern Idaho, Arizona; Bazilevich 1994). Perhaps higher productivity forests have more abundant prey following disturbance than lower productivity forests (Huston 1994, Kondoh 2001), which may offset negative effects of disturbance on goshawk reproductive success. Alternatively, natural disturbance regimes in higher productivity forests are often characterized by mixed-severity and stand-replacing fires, as opposed to low-severity surface fires in drier forests (Smith and Fischer 1997). Goshawk populations would be expected to evolve accordingly and become more adapted to the heterogeneous environments resulting from periodic stand-replacing events.

A more likely explanation for both temporal and spatial variability in goshawk reproduction is that a combination of factors is responsible. We found goshawk reproduction to be related to both habitat and weather variables. As long as goshawks have a suitable amount of nesting habitat within their territory, weather may become the primary factor related to reproductive success. Cold, wet weather may directly affect goshawk reproduction by reducing breeding activity (Newton 1979) and nesting success (Kruger and Lindstrom 2001). In addition, adverse weather could presumably affect hunting success and prey

densities and availability. Prey availability in turn can affect both goshawk territory reoccupancy (Doyle and Smith 1994) and productivity (Doyle and Smith 1994, Salafsky et al. 2005). Doyle and Smith (1994) found that goshawk reproduction was strongly related to snowshoe hare (*Lepus americanus*) density in the Yukon Territory. Similarly, Salafsky et al. (2005) found a strong relationship between goshawk productivity on the Kaibab Plateau of Arizona and red squirrel (*Tamiasciurus hudsonicus*) abundance. Low prey populations can reduce the number of goshawk breeding pairs (Linden and Wikman 1983).

Some caution should be used when interpreting our results because we only monitored territories for 2 breeding seasons following timber harvest. It is possible that negative effects may only become apparent after long-term monitoring. We also did not follow marked birds, so turnover rates of individuals were not known. Furthermore, our sample sizes were relatively small without randomly-assigned treatments; therefore inference may not be strong outside of our sample population or to other years. Also, detection of goshawks may be biased towards territories that have had timber harvest because these territories may be easier to search due to the reduction of suitable nesting habitat. Lastly, weather data often have a large variance and caution should be used in the interpretation of models constructed with these variables, particularly when the models are built from weather data from a short time period.

MANAGEMENT IMPLICATIONS

Current forest management guidelines developed for the southwestern U.S. recommend no commercial timber harvest within a 12-ha goshawk nesting area and at least 60% of the 170-ha area surrounding the nest in equal portions of vegetation structural stages 4-6 (Reynolds et al. 1992). Because no published guidelines exist for mesic forests in the

northern Rocky Mountain region, management principles from the southwestern guidelines have often been applied. However, we have found that timber harvest can be implemented within territories after the post-fledging dependency period, which is approximately 15 August in this region, with no significant adverse effects on subsequent year's reproduction as long as >39% of the 170-ha territory is left in vegetation structural stages 4, 5, or 6 with a canopy closure >70%. However, because mean nesting habitat in reoccupied territories was 57-58%, we recommend leaving amounts of nesting habitat >50% in the nesting territory to increase the probability of reoccupancy. We also recommend long-term monitoring of goshawk reproduction when conducting forest management activities within territories.

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Table 1. Habitat and weather variables used to develop classification tree models to predict goshawk territory reoccupancy and nesting success, Idaho, 2001-2004.

Variable	Description	Reoccupancy	Success	
Treatment	ent Timber harvest versus no harvest		X	
Year postharvest	Time following timber harvest	X	X	
Preharvest habitat	Percentage of territory in potential	X		
	nesting habitat before timber harvest			
Postharvest habitat	Percentage of territory in potential	X	X	
	nesting habitat after timber harvest			
Jan precip	January mean daily precipitation	X	X	
Feb precip	February mean daily precipitation	X	X	
Mar precip	March mean daily precipitation	X	X	
Apr precip	April mean daily precipitation		X	
May precip	May mean daily precipitation		X	
Jan max temp	January mean daily maximum temp	X	X	
Feb max temp	February mean daily maximum temp	X	X	
Mar max temp	March mean daily maximum temp	X	X	
Apr max temp	April mean daily maximum temp		X	
May max temp	May mean daily maximum temp		X	

Table 2. Mean (SD) goshawk productivity, reoccupancy, and nesting success for 1 and 2 years following timber harvest treatments, Idaho, 2001-2004.

Treatment	Year	Reoccupancy	Success	Productivity (All nests)	Productivity (Successful nests)
Harvested	1	10/11	7/11	1.0 (0.9)	1.6 (0.5)
	2	8/11	4/11	1.2 (1.3)	2.3 (0.6)
Unharvested	1	8/10	6/10	1.3 (1.2)	2.2 (0.4)
	2	8/10	3/10	0.5 (0.8)	1.7 (0.6)

Table 3. Mean (SD) proportion of 170 ha goshawk territories in suitable nesting habitat before and after timber harvest, Idaho, 2001-2004.

	Proportion preharvest	Proportion postharvest	
Nesting status	nesting habitat	nesting habitat	
Year 1			
Occupied $(n = 18)$	0.70 (0.17)	0.57 (0.16)	
Unoccupied $(n = 3)$	0.50 (0.15)	0.35 (0.15)	
Successful $(n = 13)$	0.71 (0.20)	0.56 (0.19)	
Unsuccessful $(n = 7)$	0.61 (0.13)	0.50 (0.15)	
Year 2			
Occupied $(n = 16)$	0.68 (0.19)	0.58 (0.19)	
Unoccupied $(n = 3)$	0.59 (0.19)	0.43 (0.18)	
Successful $(n = 7)$	0.67 (0.21)	0.54 (0.21)	
Unsuccessful $(n = 4)$	0.66 (0.19)	0.55 (0.21)	
Year 1 and 2			
Occupied $(n = 34)$	0.69 (0.18)	0.57 (0.17)	
Unoccupied $(n = 8)$	0.55 (0.17)	0.39 (0.16)	
Successful $(n = 20)$	0.69 (0.20)	0.55 (0.19)	
Unsuccessful $(n = 22)$	0.63 (0.16)	0.53 (0.18)	

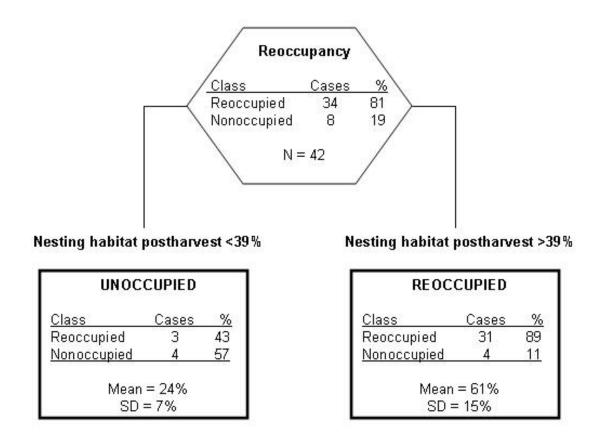


Figure 1. Classification tree for predicting goshawk territory reoccupancy. Reoccupancy is predicted by the amount of potential nesting habitat remaining within the territory after timber harvest. The mean (SD) amount of nesting habitat remaining postharvest is given for the cases in each node.

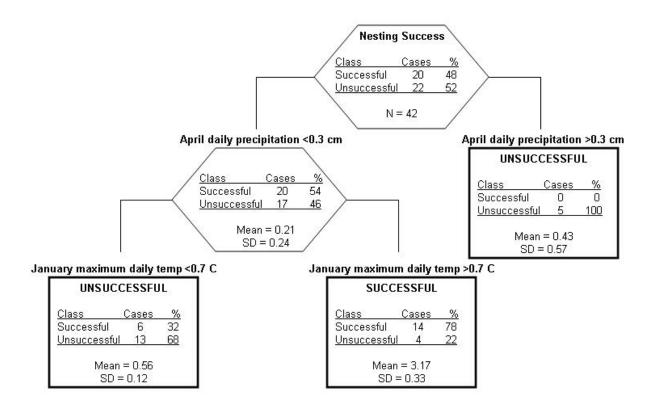


Figure 2. Classification tree for predicting goshawk nesting success. Nest success is predicted by a combination of April daily precipitation and January maximum daily temperature. The mean and standard deviation for each significant weather variable are provided in each node.

Chapter 3. Effects of Telemetry Location Error on Space-Use Estimates Using a Fixed-Kernel Density Estimator

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ABSTRACT Fixed-kernel density estimates using radio-telemetry locations are frequently used to quantify home ranges of animals, interactions, and resource selection. However, all telemetry data have location error and no researchers have reported the effects of error on utilization distribution and area estimates using fixed-kernel density estimators. We simulated different home range sizes and shapes by mixing bivariate-normal distributions and then drawing random samples of various sizes from these distributions. We compared fixed-kernel density estimates with and without error to the true underlying distributions. The effects of telemetry error on fixed-kernel density estimates were related to sample size, distribution complexity, and ratio of median circular error probable (CEP_{0.50}) to home range size. We suggest a metric, the ratio of telemetry error to home range size, to assess the adequacy of the telemetry system being used to estimate an animal's space use before a study is undertaken. Telemetry-location error is unlikely to significantly affect fixed-kernel density estimates for most wildlife-telemetry studies with adequate sample sizes.

KEY WORDS cross validation, error ratio, fixed kernel, home range, location error, radio telemetry, space use, utilization distribution.

An animal's space use is often studied using radio telemetry to obtain locations during a specified time period. These locations can then be used to quantify aspects of space use using a variety of estimators. One of the most common space-use estimators in wildlife studies today is the fixed-kernel density estimator (hereafter fixed kernel). Fixed kernels have been used to estimate animal home ranges (Worton 1989), interactions (Millspaugh et al. 2004), and resource selection (Marzluff et al. 2004, Millspaugh et al. 2006).

The properties of fixed kernels have been well studied (e.g., Worton 1989, Seaman and Powell 1996, Seaman et al. 1999). The fixed kernel has superior properties compared to other home range estimators because it 1) is non-parametric, 2) is unbiased, 3) calculates an animal's utilization distribution (UD), 4) is robust to autocorrelation, and 5) is not sensitive to outliers (Kernohan et al. 2001). Some authors have also suggested that fixed kernels are relatively robust to telemetry error compared to other space-use estimators (e.g., Marzluff et al. 2001). Although this seems logical given the smoothing function of the kernel, no published studies have assessed the effects of telemetry error on fixed-kernel estimates. Telemetry error has the potential to affect the extent and shape of the UD. Although a few small location errors would likely have little impact on the UD, large, systemic location error could alter the size and shape of the UD, thus affecting estimates of home range, animal interactions, and resource selection.

Telemetry error is frequently unreported in animal space use studies. Hupp and Ratti (1983) were one of the first to note that 75% of radio telemetry papers did not report location

error. Although this rate has improved over the last 20 years, Withey et al. (2001) found that nearly half of all radio-telemetry studies recently published in the *Journal of Wildlife*Management inadequately reported telemetry error or did not report it at all, suggesting these studies either did not consider telemetry error to be an important factor in their space-use estimates or did not know how to deal with error. Our objective was to provide a tool to assess the effects of telemetry error when using fixed kernels to estimate animal space use.

METHODS

Telemetry Error

We developed an error ratio (ER) that relates telemetry error to the size of the home range. The ER is defined as:

$$ER = CEP_{0.50}/A$$

where CEP_{0.50} is the median circular error probable (Moen et al. 1997), which is the circle with a radius around a known location that contains 50% of the test locations, and A is the approximate home-range area of the animal under study. We use the median-location error rather than the mean because the mean is a poor estimator of central tendency for telemetry-location error when errors are not normally distributed. The ER must be expressed in similar units (e.g., m/m²). This ratio can usually be estimated before a study is initiated because most researchers know or can estimate the average error of the telemetry system they are using, and can also estimate the size and complexity of the animal's home range they are studying from published literature or pilot studies.

Simulations

We simulated UDs that represented various levels of space-use complexity, similar to previous studies (Seaman and Powell 1996, Seaman et al. 1999, Horne and Garton 2006). We used mixtures of bivariate-normal distributions to create 1-, 4-, and 8-mode UDs. We found in pilot simulations that greater complexity, defined by the number of modes in a UD, did not contribute substantial information. Thus we limited our study to the 3 mixtures above. We randomly selected parameter values from normal distributions with mean (x, y) from 0 to 20, standard deviation from 1.5 to 6, covariance -1 to 1, and we selected mixing proportions from 0 to 1 with the constraint that the proportions summed to 1 (Horne and Garton 2006).

We simulated 40 realizations for each of the 3 types of bivariate-normal mixes by randomly selecting different parameter values for each realization. We drew random samples of 25, 50, 100, 250, and 500 points from each realization to simulate telemetry locations. We replicated each sample size 100 times for each of the 40 realizations and 3 bivariate mixes, for a total of 60,000 simulated location samples. We simulated location error by adding random numbers to (x, y) sample coordinates drawn from the true distributions. Errors were randomly selected from normal distributions with (x, y) mean 0 and standard deviations ranging from 1 to 250. We used ArcView 3.2 Geographic Information System (GIS) to estimate the median-location error resulting from adding random error values to the (x, y)sample coordinates, and then we calculated error ratios based on the median error and the 95% true distribution extents. Error ratios of simulated distributions ranged from 0 to 0.20 and we sorted and binned them according to the following intervals: 0, 0.001 to 0.009, 0.010 to 0.049, and 0.050 to 0.200. We used the no-error category as a reference. We set the lowest error ratio at the interval 0.001 to 0.009 by reviewing a broad suite of telemetry studies and determining ERs for the telemetry systems and animals under study. Most wildlife telemetry

studies fell within this interval. We set the interval 0.010 to 0.049 because it represented some telemetry studies with high ERs such as might be found using relatively inaccurate telemetry systems, and the interval 0.050 to 0.200 because it represented extreme cases with telemetry error that would probably be considered unacceptable to most researchers interested in accurately estimating home range sizes.

Kernel Calculations

We calculated fixed-kernel density estimates for each sample using a standard bivariate-normal kernel (Silverman 1986). Fixed kernels are sensitive to the type of smoothing factor or bandwidth values (Silverman 1986). Several bandwidth-selection procedures have been evaluated for use in fixed-kernel estimates, and least-squares cross-validation (LSCV $_h$) is the most widely accepted (Seaman and Powell 1996). However, several new bandwidth-selection procedures have recently been evaluated and shown to perform well (Gitzen et al. 2006, Horne and Garton 2006). No single smoothing parameter is likely to perform well in all conditions. Therefore, we used 2 automatic methods for choosing the smoothing parameter. For smoothing, we chose LSCV $_h$, because it is the most widely-used method and generally performs well with sample sizes \geq 50 (Seaman et al. 1999, Horne and Garton 2006), and likelihood cross-validation (CV $_h$) because it has been shown to be a better procedure for small sample sizes and for obtaining more accurate estimates in high-use areas (Horne and Garton 2006). For each bandwidth method we simulated 60,000 home ranges for a total of 120,000 fixed-kernel UDs.

Comparisons

We compared the fixed-kernel estimates from each sample using both bandwidthselection procedures to the true distribution using 2 measures. We used the volume of intersection (VI) index to assess the fit of the sample UD to the true UD (Seidel 1992, Millspaugh et al. 2004). The VI is a value between zero (no overlap) and 100 (complete overlap) and is an easily interpreted metric of how well the estimated UD fits the true UD. The VI is calculated by summing the UD volume shared by 2 distributions. The amount of shared volume within each pixel of the evaluation grid is summed to obtain the VI. The VI is defined as:

$$\left[VI = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \min \left[f_1(x, y), \hat{f}_2(x, y) \right] dx dy \times 100 \right]$$

where f_1 is the true mixture distribution and \hat{f}_2 is the estimated distribution. The VI can be used to assess how well a kernel estimates the intensity or probability of space use because it is most sensitive to discrepancies where the UD density is highest, such as the inner contours of fixed-kernel estimates. We assessed the VI over a grid of points bounded by the 99.9% contour of the UDs.

We also compared areas associated with the 50% and 95% contours of the sample UDs (Â) versus the true distributions (A) using percent relative bias (PRB) defined as:

$$PRB = (\hat{A} - A)/A \times 100$$

The 50% contour is often used as an estimate of an animal's core-use area (Samuel et al. 1985), whereas the 95% contour is commonly used as an estimate of an animal's home range (Kernohan et al. 2001). Bias in the 50% contour may result in a poor estimate of space use

within the core area, whereas bias in the 95% contour may lead to an inaccurate depiction of an animal's home-range size. Positive bias would indicate an overestimate of area, whereas negative bias would indicate an underestimate of the area.

We graphically compared mean VI and PRB of all estimated UDs with and without error to the true distributions. Of particular interest was how well kernel UDs estimated with location error performed compared to kernel UDs estimated without location error. Of secondary interest was how well kernel UDs estimated without location error performed compared to true UDs. We computed all simulations and calculations using Visual Basic 6.0 (Microsoft Corporation, Redmond, WA).

Case Study

We wanted to assess the effectiveness of using satellite platform transmitter terminals (PTTs) and the Argos system to estimate space use of the northern goshawk (*Accipiter gentilis*), a central-place forager that likely has a unimodal UD during the breeding season. We placed 20-g and 30-g PTTs (North Star Science and Technology, King George, VA) at 65 locations systematically spaced in a forested landscape in northern Idaho to test PTT accuracy across a variety of forest cover types and topography. We generated beacon locations in a geographic information system (GIS) and identified them on the ground using aerial photographs and a global positioning system (GPS). We placed a PTT in the field at a beacon for one 12-hr duty cycle. We conducted all tests in 2005 after Argos implemented a new algorithm incorporating digital elevation models in the location calculations. Because previous researchers have demonstrated Argos location class 1s to be highly inaccurate (e.g., >1,000 m; Keating et al. 1991), we considered only the more accurate location class 2 and 3s for the error analysis.

RESULTS

Simulations

The effects of telemetry error on fixed-kernel UD and area estimates were similar between the 2 bandwidth selection methods. Mean VI scores differed by <1% for the 2 methods, and mean percent relative bias differed by <5%. Therefore, to conserve space and simplify the results we present graphs for only the CV_h bandwidth-selection method.

For all comparisons, VI scores increased with sample size and decreased with increasing ER (Fig. 1). Location error had a relatively small effect on VI for 1-mode distributions except at the highest ER (Fig. 1a). However, even at the highest error level VI scores were only reduced by approximately 5%. At the lowest error level, volume of intersection scores passed the 80% mark at sample sizes of \geq 50 and increased to approximately 90% for n = 500.

Location error had a more marked effect on VI scores for the more complex distributions (Fig. 1b,c). Fixed-kernel estimates, however, performed better with telemetry error for the 8-mode relative to the 4-mode distributions. VI scores reached 80% for no error and low ER values at n > 175 for the 8-mode distributions. Scores failed to reach 80% even at n = 500 for the 2 highest ERs for the 4-mode distributions.

For all 95% contour comparisons, percent relative bias decreased with sample size and increased with increasing ER (Fig. 2). The lowest level of telemetry error had a <4% positive relative bias effect on 95% contour estimates for 1-mode distributions compared to no error estimates (Fig. 2a). The highest error level resulted in a <10% positive relative bias for all sample sizes compared to the no error estimates. Relative bias decreased for all levels of error with increasing sample sizes (Fig 2a.)

More complex distributions resulted in higher levels of relative bias (Fig. 2). The percent relative bias caused by the low ER in 4-mode distributions was <20% for sample sizes compared to the no error estimates. The higher ERs resulted in relative bias >40% across all sample sizes compared to the no error estimates (Fig. 2b). Low error in 8-mode distributions resulted in percent relative bias of <5% when n > 50 compared to no error estimates. The higher ERs resulted in positive relative bias >35% for all sample sizes when compared to no error estimates (Fig. 2c).

Patterns of relative bias were similar for the 50% contour estimates, although relative bias generally increased compared to 95% area estimates (Fig. 3). Again, percent relative bias decreased with sample size and increased with increasing ER (Fig. 3). Low ER did not affect estimates for 1-,4-, or 8-mode distributions by >10% when compared to no error estimates (Fig 3). However, the higher ERs in the more complex distributions resulted in positive relative bias >75% for all sample sizes when compared to the no error estimates (Fig. 3b,c).

Case Study

Our satellite PTT location class 3s and 2s had a median error of 225 m and 305 m, respectively. The combined median error for location class 2s and 3s was 254 m. Using the median error as a radius to calculate a CEP_{0.50}, and a published goshawk home range of approximately 25,000,000 m² (Squires and Reynolds 1997), the calculated ERs for location class 3s, 2s, and combined were 0.006, 0.012, and 0.008, respectively. Based upon our simulations we determined that location error for both location class 2s and 3s was unlikely to affect our fixed-kernel space use estimates by >10% regardless of the metric used to judge

the estimates.

DISCUSSION

Error ratios for most telemetry studies are below the 0.01 limit that we demonstrated had a relatively small effect on fixed-kernel density estimates. Studies using telemetry systems with a relatively high median location error may be appropriate as long as the home range is large, relative to the size of the CEP_{0.50}. Our case study using PTTs designed for use on northern goshawks is a good example because the Argos system is one of the least accurate telemetry systems available (Rodgers 2001). However, the northern goshawk is a relatively wide-ranging central-place forager (Squires and Reynolds 1997), which mitigates the effects of location error. On the other hand, a species with a small home range relative to CEP_{0.50} would require a much more accurate telemetry system. A recent study by Kauhala and Tiilikainen (2002) demonstrated that the median error using very high frequency (VHF) telemetry to assess mountain hare (*Lepus timidus*) home ranges was 218 m. Using published home ranges of 113 ha for males and 89 ha for females (Hewson and Hinge 1990), the ERs would be 0.13 and 0.17, respectively. Error ratios this high would likely lead to kernel estimates that are highly inaccurate or positively biased.

Wildlife telemetry studies using GPS will probably have low ERs based on a published median location error of 5.9 m (D'Eon et al. 2002). Because most GPS transmitters are too heavy (i.e., >45 g) to go on smaller animals with relatively small home ranges, they are limited to larger animals (particularly mammals) that have larger home ranges. Because large home ranges relative to location error will result in low ERs, fixed-kernel estimates based on GPS telemetry will likely be satisfactory for most studies.

Telemetry location sample sizes >50, such as those obtained using satellite telemetry, generally lead to improved kernel estimates (Seaman et al. 1999) but can potentially lead to autocorrelation issues depending on the sampling interval (Swihart and Slade 1997). Estimates using clustered, autocorrelated points often fail to calculate an appropriate smoothing value using LSCV $_h$ (Hemson et al. 2005). In addition, n > 100 have been shown to adversely affect kernel estimates when using LSCV $_h$ (Hemson et al. 2005). Fixed-kernel density estimates using CV $_h$ tend to fail less often when points are clustered (Horne and Garton 2006). Large numbers of highly correlated locations may be better suited to space use estimators that explicitly incorporate time between successive locations, such as Brownian bridge analyses (Horne and Garton 2007).

We did not control for home range shape per se in our study, nor did we attempt to assess the accuracy of the home range shape estimates. The shape and location of fixed-kernel contours may be important for use in assessing animal interactions, habitat use, and habitat availability. Location error is likely to affect the shape and location of fixed-kernel contours and thus may affect studies that use these contours. Furthermore, although we reported effects of error relative to home range size, estimates of resources selection may be affected by absolute error, regardless of home range size. Further simulation studies could elucidate these effects on contours using Monte Carlo integration (e.g., Kong et al. 2003).

Location error is likely to affect home range estimates differently for animals that use narrow, linear landscape features compared to animals that more uniformly use a landscape (e.g., Blundell et al. 2001). Researchers should be aware that linear home ranges and/or those with multiple linear features will be sensitive to location error, and our results may not be as applicable.

Accurate fixed-kernel estimates are also influenced by sample size. Sample sizes of ≥ 50 appear to be appropriate for most telemetry studies, although our estimates generally continued to improve to n = 500. Although large sample sizes may be difficult to obtain in studies using VHF telemetry, they are more easily obtained using satellite telemetry and we recommend them as long as serial correlation does not adversely affect estimates and study objectives (Hemson et al. 2005).

Simulation studies such as ours are useful for understanding real-world phenomena. Yet, it is impossible to simulate all estimators, field conditions and telemetry systems. We simplified our simulations to make analyses and interpretations easier. Many types of kernel estimators are available, and their use may lead to different conclusions than ours. In addition, real telemetry error may not be distributed the same as our simulated locations. We recommend researchers seek to understand the estimator they are using, the properties of their data, and how both of these might affect their space-use estimates, including estimates of the UD, home range area, and contour shape and placement.

MANAGEMENT IMPLICATIONS

We have provided wildlife researchers with a tool, the ER, to evaluate the effects of telemetry error on fixed-kernel density estimates before a telemetry study is undertaken. We demonstrated that the level of location error found in most telemetry studies will not greatly affect fixed-kernel UD and contour-area estimates. However, researchers must determine the acceptable level of telemetry error based on the objectives of their study. In addition, all telemetry studies should estimate and report location error, and median error is a more appropriate measure of central tendency than the mean when the distribution of location errors is skewed. Using the median location error to compute the CEP_{0.50} and an a priori

estimate of an animal's home range, researchers can determine whether the expected fixedkernel estimates are suitable for their study objectives.

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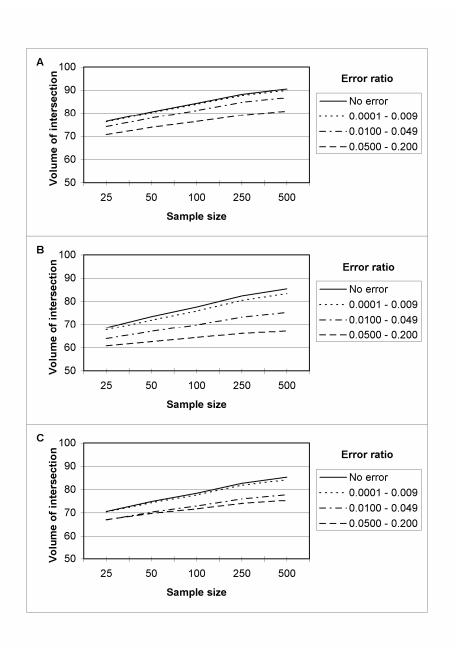


Figure 1. The effects of telemetry location error on volume of intersection scores for A) 1-mode mixtures, B) 4-mode mixtures, and C) 8-mode mixtures. We did not include standard errors in figures because they were too small to display due to the large sample sizes.

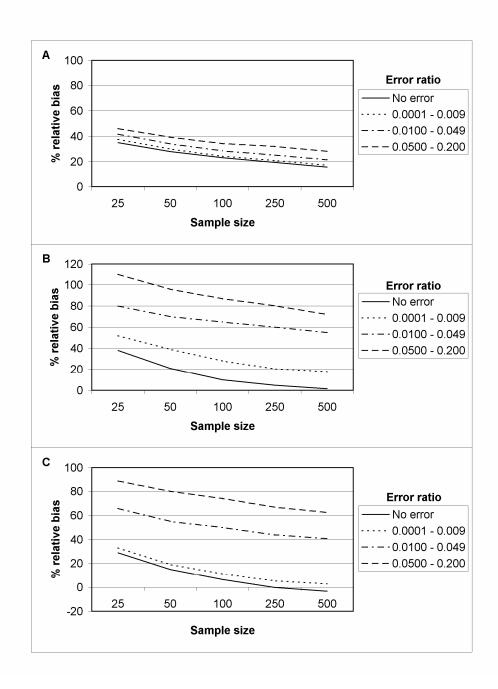


Figure 2. The effects of telemetry location error on percent relative bias for 95% fixed-kernel contour area estimates for A) 1-mode mixtures, B) 4-mode mixtures, and C) 8-mode mixtures. We did not include standard errors in figures because they were too small to display due to the large sample sizes.

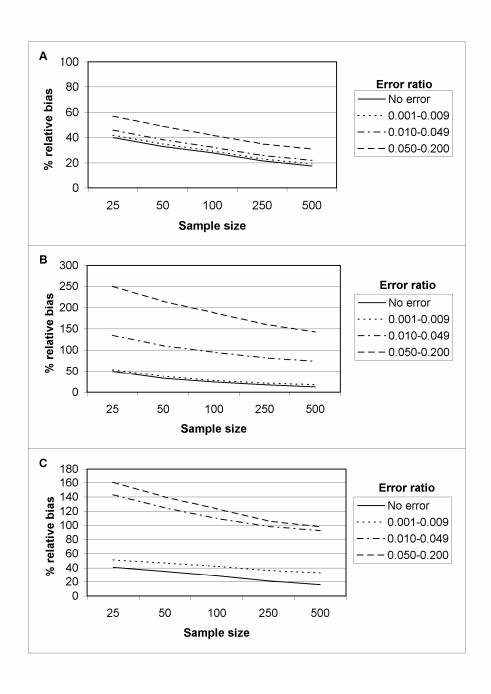


Figure 3. The effects of telemetry location error on percent relative bias for 50% fixed-kernel area estimates for A) 1-mode mixtures, B) 4-mode mixtures, and C) 8-mode mixtures. We did not include standard errors in figures because they were too small to display due to the large sample sizes.

Chapter 4. Estimating Northern Goshawk Space Use, Territory Fidelity, and Residency Status Using Satellite Telemetry

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ABSTRACT Northern goshawk (*Accipiter gentilis*) space use has not been previously reported for the northern Rocky Mountains. We captured male (n = 7) and female (n = 12)goshawks during the nesting season in 2004 and 2005 and fitted them with satellite platform transmitter terminals (PTTs) using backpack harnesses. Mean ± SE male and female breeding-season home ranges using 95% fixed-kernel estimates were 5146 \pm 826 and 3859 \pm 815 ha, respectively. Mean ± SE male and female breeding-season core-use areas using 50% fixed-kernel estimates were 1172 ± 210 and 762 ± 156 ha, respectively. Mean \pm SE female home ranges during the nonbreeding season using 95% fixed-kernel estimates were 9251 \pm 1743 ha, while core-use areas were 2676 ± 685 ha. Failed nesting attempts resulted in significant increases in home ranges and core-use areas for both males and females. Linear regression models suggested home range size was a function of both nesting success and habitat within the home range. Female goshawks were year-round residents in this study and centered their nonbreeding season activity within 10.4 ± 5.1 km of their nest. Nine of 10 females switched territories in the year following radio-tagging. Goshawks in this region may have larger home ranges and lower female fidelity to territories than documented elsewhere.

KEY WORDS *Accipiter gentilis*, core-use area, fixed-kernel, home range, northern goshawk, satellite telemetry, space use, territory

The northern goshawk (*Accipiter gentilis*) is a wide-ranging central-place forager during the breeding season (Squires and Reynolds 1997). Although no data exist on goshawk breeding-season home ranges in the northern Rocky Mountain region, other studies throughout the goshawk's range have reported home ranges between 570 and 5344 ha (Squires and Reynolds 1997, Boal et al. 2003). Goshawk home ranges within a region are variable, particularly by sex because the male does most of the provisioning during the nesting period (Younk and Bechard 1994). Thus, male home ranges are usually larger than females during this time period (Squires and Reynolds 1997). Other factors potentially contributing to the variability of home range sizes include prey densities and habitat characteristics (Kenward 1982).

The characteristics of goshawk space use during the nonbreeding season are also variable (Squires and Reynolds 1997). Some breeding populations remain near the territory even during the winter (Boal et al. 2003). However, most populations are considered partially migratory, meaning migration is related to temporal fluctuations in weather or prey availability (Doyle and Smith 1994, Sonsthagen et al. 2006, Underwood et al. 2006). Fluctuations in weather and prey can lead to irruptions of fall migrants, particularly juveniles (Doyle and Smith 1994, Hoffman and Smith 2003).

Satellite telemetry is a useful tool for assessing space use in a wide-ranging bird because unlike telemetry studies using very-high-frequency (VHF) telemetry, birds can be tracked even if they leave the study area. This allows not only for home-range estimates, but

also for an assessment of migratory status and other long-range movements. Furthermore, other behaviors such as territory fidelity can be assessed concurrently. The objectives of our study were to use satellite telemetry to estimate goshawk breeding- and nonbreeding-season home ranges, migratory status, and territory fidelity in northern Idaho.

STUDY AREA

Our study took place within an 890,000-ha region of the Clearwater Mountains in northern Idaho, bounded in the south by the Middle Fork Clearwater River and in the north by the St. Joe River. Elevations ranged from 750-1500 m and annual precipitation ranged from 75-125 cm. Forests in this region are managed primarily for timber production, and the 3 primary landowners were Potlatch Forest Holdings, Inc., Idaho Department of Lands, and the U.S. Forest Service (Clearwater National Forest and Idaho Panhandle National Forest). Although forest types ranged from dry ponderosa pine (*Pinus ponderosa*) to cold subalpine fir (Abies lasiocarpa) habitat types, over 85% of the landscape consisted of mesic western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) habitat types (Cooper et al. 1991). This landscape has a history of both natural and anthropogenic disturbance. Prior to European settlement, large stand-replacing fires occurred on the order of every 150-400 years within the western redcedar and western hemlock habitat types (Smith and Fischer 1997). Although fire suppression has reduced the frequency and extent of fires more recently, these lands are highly productive and intensive timber harvest has occurred in the region for the past 100 years. These disturbances have resulted in a heterogeneous forest structure, including early to late-seral stands.

Goshawk nesting habitat in our study area has been described by Hayward and Escano (1989). Goshawks usually nest in stick platforms built against the bole of live

conifers below the canopy. Mean nest tree height is 31 m and dbh is 58 cm. Goshawks nest in closed-canopy (75-85% overstory cover) conifer forests on moderate slopes. Goshawk nest stands have a mean basal area of 40 m^2 per ha. Highest tree densities per ha are comprised of the 7.6 to 17.8 cm dbh class (mean = 475), followed by the 17.8 to 30.4 cm dbh class (mean = 265), 30.4 to 60.9 cm dbh class (mean = 175), and trees >60.9 cm dbh (mean = 20).

METHODS

Telemetry

We randomly selected goshawks to be radio-tagged from 21 territories occupied in 2004-05. We captured adult goshawks in 2004-05 during the nestling stage of the breeding season using a great horned owl (*Bubo virginianus*) and dho-gaza nets (Bloom 1987). We attached 20-g and 30-g battery-powered PTTs to male and female goshawks, respectively, using backpack harnesses. All PTTs were manufactured by North Star Science and Technology and weighed <2.8% of body weight for males and <3.2% for females. Our 30-g PTTs had a battery life of approximately 1100 hr and were programmed to cycle on from 0700 to 1900 hr every other day during the nestling and post-fledging stage (June 1-August 31) and from 0700 to 1900 hr once every 5 days during the nonbreeding season. Our 20-g PTTs had a battery life of approximately 500 hr and these units were programmed to cycle from 0700 to 1900 hr every other day during the breeding season. Thus, we monitored male goshawk space use only during the breeding season, and female space use year-round.

Space Use Estimates

We calculated home ranges using 95% fixed-kernel estimates, and core-use areas using 50% fixed-kernel estimates using the program developed by Horne and Garton (2006). We chose these contours because the 50% contour is often used as an estimate of an animal's

core-use area (Samuel et al. 1985), whereas the 95% contour is commonly used as an estimate of an animal's home range (Kernohan et al. 2001). Hereafter we refer to these spatial extents as core-use areas and home ranges. Fixed-kernel estimates are sensitive to bandwidth-selection procedures (Seaman et al. 1999). Therefore we used both least-squares cross-validation (LSCV_h) and likelihood cross-validation (CV_h) bandwidth-selection methods in our space-use estimates (Horne and Garton 2006). Home ranges were calculated only for birds with >30 locations (Seaman et al. 1999). We used only Argos' location class 2 and 3 to calculate fixed kernels, because location classes ≤ 1 have linear errors > 1 km and were considered too inaccurate to use in fixed-kernel estimates (Moser and Garton 2007). We determined median-location error of our telemetry system by placing PTTs at 65 known locations on the landscape (see Moser and Garton 2007). We assessed the potential effects of location error on our fixed-kernel estimates by computing the location error ratio as outlined in Moser and Garton (2007). The error ratio is the ratio of the median circular error probable to home-range size. The median circular error probable is the circle around a known location containing 50% of locations using a test transmitter (Moen et al. 1997). Moser and Garton (2007) demonstrated a small effect of location error on fixed-kernel estimates when the error ratio was <0.01.

Goshawk space use may be a function of factors such as nesting success and habitat quality within the home range. Nesting success may affect space use because successfully nesting birds may have a higher fidelity to the nesting area and thus a smaller home range and core-use area. We estimated the effects of nesting success on home range and core-use-area estimates. We classified a nesting attempt as successful if at least 1 nestling survived until fledging. We also modeled home range size as a function of nesting success, and

proportion of openings and closed-canopy forest in the 95% fixed-kernel home range using multiple linear regression. Proportion of the home range in openings and closed-canopy forest was calculated in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California) using Landsat 7 satellite imagery (see Moser 2007; Chapter 5). Nest success was coded 1 for successfully fledging young, and 0 if no young were fledged. We developed a set of possible models for male and female goshawks to predict home range size using various combinations of nesting success, proportion of openings, and proportion closed-canopy forest. We used Akaike's information criterion for small sample sizes (AIC_c) to compare models. Furthermore, we compared models based on the weight of evidence (w_i) and r^2 values (Burnham and Anderson 2002). We developed a single model for male goshawks and for female goshawks by averaging all of the candidate models. Models were averaged by multiplying the Akaike weights (w_i) by each model parameter and then summing the parameter values (Burnham and Anderson 2002). We developed all models using Statistix 8.0 (Analytical Software, Tallahassee, Florida).

We determined residency status and territory fidelity for female goshawks. Residency was determined by assessing distance moved from nesting areas during the nonbreeding season. Goshawks that moved >65 km were considered migratory (Squires and Ruggiero 1995). Territory fidelity was also assessed by distance moved from previous year's nest. We considered a bird to have reoccupied a new territory if the new nest was >3.8 km from the previous year's nest. We based this distance between known nearest-neighbor distances of nests in adjacent territories in this and other regions (Squires and Reynolds 1997, B.W. Moser, unpublished data). Analyses were conducted using ArcGIS 9.1. We report mean ± SE values in the results.

RESULTS

We captured 12 females and 7 males during 2004-2005. One female slipped a harness during 2005 and we were unable to obtain an adequate sample of locations for analysis during the nonbreeding season. One female and 1 male died and were recovered, and 1 PTT stopped transmitting prematurely with the cause of failure undetermined. We conducted necropsies on the dead goshawks but were unable to determine cause of death due to advanced decomposition. We were able to analyze space use during the breeding season for 12 females and 7 males, and during the nonbreeding season for 10 females. Median location error was 225 m for location class 3 and 305 m for location class 2. The combined median error for location class 2s and 3s was 254 m. The computed error ratio was < 0.006, indicating a low effect of location error on our fixed-kernel estimates.

Fixed-kernels using LSCV_h failed to calculate an appropriate smoothing factor 33% of the time, which appears to be a common problem with LSCV_h when location sample sizes are large or points are clustered (Hemson et al. 2005). However, the mean home range sizes that we were able to calculate using LSCV_h were 55% smaller than those calculated using CV_h . Hereafter we report our results using only CV_h .

Male and female home ranges during the breeding season were 4-5 times the size of their respective core-use areas during the breeding season. Male breeding-season home ranges were 33% larger than female home ranges, and male breeding-season core-use areas were 54% larger than female core-use areas. Female nonbreeding-season home ranges were 1.4 times their breeding-season home ranges. Furthermore, female core-use areas during the nonbreeding season were 2.5 times the size of those during the breeding season (Table 1).

Nesting success appeared to have a significant effect on the size of both home range and core-use areas for male and female goshawks (Table 2). Goshawks had larger home ranges and core-use areas when their nests failed to produce young. Home ranges for unsuccessful males were 74% larger than successful males during the breeding season, and core-use areas of unsuccessful males were 52% larger than successful males (Table 2). Unsuccessful female home ranges during the breeding season were 2.8 times larger than successful females, and their core-use areas were 2.5 times larger. During the winter unsuccessful female home ranges were 1.7 times and their core-use areas 2.9 times larger than successful females.

Linear regression models suggested breeding-season home range size was a function of nesting success and habitat (Table 3). The model with the lowest AIC_c that predicted male goshawk home range size included only the proportion of openings in the home range (Table 3). However, the next 3 models were competitive with Δ AIC_c <7 and higher r^2 values (Table 3). The final averaged model predicting male goshawk home range size was:

Home range (ha) =
$$3071.4 - 384.6*$$
(nest success) + $9785.8*$ (openings) – $438.0*$ (closed canopy)

This model predicted male home range size to increase with increasing amounts of open habitat within the home range and when nests fail, and decrease with increasing amounts of closed canopy forest. The proportion of openings had the strongest influence on prediction of home range size for male goshawks.

The model with the lowest AIC_c that predicted female goshawk home range size included only nest success as an explanatory variable (Table 3). However, 2 other models were competitive, with Δ AIC_c <2.1 and similar r^2 values. The final averaged model predicting male goshawk home range size was:

Home range (ha) =
$$6777.6 - 3504.4*$$
 (nest success) $-332.4*$ (openings) $-217.8*$ (closed canopy)

This model predicted female home range size to increase with decreasing nest success and decreasing proportions of both open- and closed-canopy habitat conditions. Nesting success had the strongest influence on prediction of home range size for female goshawks.

Male home ranges were generally unimodal and centered on the nest tree during the breeding season. Mean farthest male distance from the nest was 6.4 ± 1.7 km. Female home ranges were also unimodal during the nestling stage. However, some females shifted their activity centers during the post-fledging stage, resulting in a bimodal distribution. Mean farthest female distance from the nest was 8.7 ± 7.3 km, with the exception of 1 female whose nest failed in mid-June and who moved 213 km north to an area near Whitefish, Montana, only to move back to her original nesting area at the end of August.

Although female home ranges expanded significantly after 31 August (Table 1), most females appeared to be non-migratory. Most nonbreeding-season home ranges were near the nest tree, with mean farthest movements 10.4 ± 5.1 km from the nest tree. The exceptions were 2 females who moved 31 and 35 km during the winter. Female territory fidelity was

low in this study. Nine of 10 females switched territories in the year following their capture. Mean distance moved was 9.7 ± 3.0 km.

DISCUSSION

Goshawk breeding-season home ranges in this study were 2-3 times larger than those in California (Hargis et al. 1994), Arizona (Bright-Smith and Mannan 1994), and New Mexico (Kennedy et al. 1994), and comparable to those in Minnesota (Boal et al. 2003), and smaller than Alaska (Iverson et al. 1996). However some of these authors only tracked goshawks during the nestling stage, which may explain why our home range sizes were larger. Goshawks tend to expand their home ranges during the post-fledging stage of the breeding season (Hargis et al. 1994). Nonbreeding-season home ranges for females were 2-3 times higher than those reported in Utah (Sonsthagen et al. 2006) and California (Keane and Morrison 1994). Female nonbreeding-season home ranges have not been studied elsewhere in the United States. We would expect nonbreeding-season home ranges to be larger than those of breeding-season home ranges because there should be less fidelity to a nesting area, because adults no longer have to provision young and reduced prey densities may force goshawks to range farther for food.

Goshawk core-use areas have not been reported frequently in space-use studies.

Kennedy et al. (1994) reported core-use areas in New Mexico using the 32% isopleths resulting from harmonic-mean estimates. They found core-use areas to be much smaller than ours. However, this may be at least partially due to the difference in methodology between the studies.

We found goshawk home range size to be a function of both nesting success and resource availability. Others have also found that goshawk home-range size was correlated

with the amount of foraging habitat within the home range (Kenward and Widen 1989). Similarly, home-range size may also be a function of prey availability (Kenward 1982), which may vary both temporally and spatially. Bloxton (2002) found that cold, wet weather resulted in reduced prey density, which was inversely related with goshawk home range sizes in western Washington. We did not assess the effects of weather or prey availability on goshawk home range size in our study.

Temporal fluctuations in prey abundance have also been cited as the primary reason for migratory behavior in goshawks (Doyle and Smith 1994). Because our study only assessed migratory behavior for 2 years, it is possible that we may not have adequately sampled across enough years to demonstrate permanent residency. Goshawks in our region may in fact migrate when prey abundance fluctuates below a certain level, making them partial migrants (Squires and Reynolds 1997).

Home-range estimates from different studies may vary depending on the type of estimator used. Minimum convex polygons (MCPs) were commonly used in earlier goshawk space use studies, but MCPs are positively biased with sample size and therefore are usually not comparable among studies (Kernohan et al. 2001). Fixed-kernel methods have become common in more recent studies, but fixed-kernel estimates can also vary depending on the smoothing factor that is used (Gitzen et al. 2006, Horne and Garton 2006). However, fixed-kernel estimates are relatively unbiased and are not as sensitive to sample size as MCPs (Kernohan et al. 2001). Home range size can differ depending on the type of smoothing factor used in a kernel analysis (Horne and Garton 2006). Fixed kernels estimated using CV_h can be larger than those computed using $LSCV_h$. In fact, when we computed 95% fixed kernels for some of our goshawk locations using $LSCV_h$, we found that mean home ranges

were 55% smaller than those computed with CV_h . Therefore, our estimates of goshawk home ranges in fact may be more comparable to those from other populations.

Most female goshawks stayed within 10.4 km of their nest tree and appeared to be year-round residents. Only 2 females moved >30km from their nesting area. Such distances are considered by some authors to be normal for wide-ranging resident birds (Squires and Ruggiero 1995, Sonsthagen et al. 2006). Squires and Ruggiero (1995) found that migratory goshawks (n = 4) breeding in Wyoming moved >65 km from their nesting area. Underwood et al. (2006) found that migratory behavior was variable among female goshawks in Utah. They hypothesized temporal and spatial variability in prey availability might explain the differences among individuals and years.

One of the advantages of the fixed-kernel home-range estimator is that it computes an animal's utilization distribution. The utilization distribution is a probability density function that predicts an animal's location anywhere within its home range. Areas with higher densities of locations will result in higher probabilities of use as estimated by the utilization distribution. It is assumed that the home range of a goshawk is an approximation of the foraging habitat (Squires and Reynolds 1997). The utilization distribution of a central-place forager such as a goshawk will have high probabilities of use near the nest site. This may be more of a result of the bird's behavior of repeatedly returning to the nesting area to deliver prey than it is a function of foraging habitat selection (Rosenberg and McKelvey 1999). Thus the estimate of a goshawk's core-use area during the nesting season may be an overestimate of the importance of this area as foraging habitat. In fact, the outlying parts of a goshawk home range may be important foraging areas whose probabilities of use may not reflect this importance (Moser 2007, Chapter 5). This is due to the effects of central-place foraging

behavior during the breeding season that tends to bias space use near the nest site even though the birds may be foraging or engaging in other behaviors away from the nest (Rosenberg and McKelvey 1999).

We found that female goshawks had a low fidelity to territories during our study period. Others have noted that female fidelity to territories was slightly lower than male fidelity (Detrich and Woodbridge 1994). Most of the males in our study were unmarked so we were unable to assess male fidelity to territories. However, high female turnover may indicate a strategy by females to diversify their mate choice and thus the genetic structure of their offspring, which has been demonstrated to increase fitness correlates such as clutch size in other species (Tomiuk et al. 2007). Alternatively, goshawks whose nests fail or whose nesting habitat is disturbed may have a higher tendency to move to another territory. However, only 2 of the nesting territories received any type of timber harvest after the breeding season when the females were radio tagged, and 1 of these birds moved and another stayed on the same territory the following year.

Limitations of our study include small sample sizes and short study duration. In addition, we were unable to monitor males beyond the breeding season due to short battery life of our 20-g PTTs. The variance around our home-range estimates was large, indicating a high amount of variability among individuals. Future studies would benefit from larger sample sizes and a longer sampling period.

MANAGEMENT IMPLICATIONS

Goshawks in this region have relatively large home ranges that are centered around their nest areas year-round. The habitats within these home ranges may be even more important for conservation than if goshawks only used them during the breeding season.

Although we did not assess habitat selection in this study, we did determine that goshawk home range sizes are related to both nesting success and the proportion of openings and closed-canopy forest within the home range. Larger home range sizes are costly to traverse and defend and may reduce goshawk fitness. Although we did not determine a threshold for the optimal proportion of openings in a landscape, land managers should seek to balance timber harvest and the amount of forest openings on the landscape with closed-canopy forest conditions.

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Table 1. Mean \pm SE goshawk telemetry sample sizes and space use estimates (ha) using 50% and 95% fixed-kernels, Idaho, 2004-2005.

		Location	95%	50%
Sex (n)	Season	sample size	Home range	Core-use area
Male (7)	Breeding	61 ± 22	5146 ± 826	1172 ± 210
Female (12)	Breeding	80 ± 49	3859 ± 815	762 ± 156
(10)	Nonbreeding	111 ± 38	9251 ± 1745	2676 ± 683

Table 2. Mean \pm SE goshawk 95% home range (ha) and 50% core-use area (ha) estimates for successful versus unsuccessful nests, Idaho, 2004-2005.

Sex	Season	Nesting status	n	95% Home range	50% Core-use area
Male	Breeding	Successful	4	3910 ± 488	841 ± 41
		Unsuccessful	3	6793 ± 1389	1276 ± 367
Female	Breeding	Successful	8	2672 ± 645	512 ± 147
		Unsuccessful	4	7421 ± 1074	1263 ± 201
	Nonbreeding	Successful	8	7954 ± 2084	1718 ± 414
		Unsuccessful	2	13788 ± 1282	4911 ± 1815

Table 3. Comparison of linear regression models used to predict goshawk home range size during the breeding season, Idaho, 2004-2005. Signs before variables indicate the relationship of each variable with home range size.

Sex	Model	AIC	ΔAIC _c	W_i	C4.	Adjusted r ²
Male	+ Openings	43.2	0.0	0.818	0.49	0.39
	- Nest success, + openings	48.2	5.0	0.069	98.0	0.80
	- Nest success, - closed canopy	49.7	6.5	0.031	0.78	99.0
	- Nest success, + openings, + closed canopy	50.2	6.9	0.026	0.87	0.73
	- Nest success	50.2	7.0	0.025	0.50	0.40
	- Closed canopy	50.5	7.2	0.022	0.45	0.34
	- Closed canopy, + openings	52.2	8.9	0.009	0.50	0.26
Female	- Nest success	86.3	0.0	0.388	0.40	0.33
	- Nest success, + openings	88.2	2.0	0.146	0.40	0.26
	- Nest success, + closed canopy	88.3	2.1	0.143	0.40	0.26
	+ Openings	88.7	2.5	0.113	0.03	-0.07
	- Closed canopy	88.8	2.6	0.108	0.01	-0.09
	- Nest success, + openings, + closed canopy	90.2	3.9	0.056	0.40	0.18
	- Closed canopy, - openings	90.5	4.2	0.047	0.07	-0.13

Chapter 5. Estimating Resource Selection: Correcting for Behavior Associated with Central-Place Foraging

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ABSTRACT Resource-selection studies often use samples of animal locations to estimate resource use. Nearly all resource-selection models assume that space use is uniform. However, in the case of central-place foragers, the null utilization distribution (UD) is not uniform but rather a circular-normal distribution centered about the central place. Estimating resource selection without correcting for the behavior associated with central-place-foraging will result in models biased towards habitats closest to the central place. We present a model for estimating a resource-utilization function (RUF) that explicitly accounts for central-placeforaging behavior and provides a more accurate picture of resource use when using UDs to measure resource use. The bias-corrected RUF uses a fixed-kernel-density estimator to calculate a UD, and then uses the difference between the surface of this UD and the surface of a circular-normal UD to calculate corrected space-use probabilities. The individual UD cell probabilities can then be used as a response variable in a modeling framework to identify variables that best explain space use. We demonstrate the use of bias-corrected RUFs using telemetry data from northern goshawks breeding in northern Idaho. Uncorrected and biascorrected UDs were used as response variables in regression tree analyses. Although

uncorrected RUFs with distance to nest as a predictor variable had lower error than biascorrected models, the distance-to-nest variable masked the effects of selection for features
away from the nest such as elevation, distance to stream, and distance to ridgetops, as
demonstrated by the bias-corrected model. Advantages of the bias-corrected RUF include a
less-biased picture of habitat selection by central-place foragers and the ability to map
goshawk habitat using the resulting model without first needing to know nest-site locations.

KEY WORDS *Accipiter gentilis*, bias-corrected RUF, central-place forager, CART, habitat selection, northern goshawk, regression tree, resource-utilization function, utilization distribution.

Resources are necessary to sustain wildlife populations, and therefore it is important to understand animal habitat use. A number of analytical techniques are available to estimate habitat selection (Alldredge and Ratti 1986, 1992, Manly et al. 2002). However, most of these techniques assume the null space-use model to be a uniform distribution. In other words, given homogeneous habitat, no central place, and no interactions with other animals, it is assumed that an animal will wander randomly through space. The assumptions for this null model are rarely met. Animal interactions such as competition and predation do occur. In addition, many animals have central locations such as den or nest sites to which they repeatedly return. The null space-use model that includes these types of behaviors is not a uniform distribution. In order to estimate selection for particular habitats, these other behaviors must be factored out or accounted for in the habitat-selection model.

Central-place foraging theory assumes that each foraging trip begins and ends at a central place (Okubo 1977). An animal leaves the nest to forage and at some point acquires prey and returns to the central place. The null model of random walks from a central place and back results in a circular-normal distribution (Fig. 1B) because space use is inversely related with increasing distance from the central place. If intra- or interspecific interactions were added to the model, the bivariate-normal may become the best null model because it could contract along the x- or y-axis as necessary to account for avoidance of or competition with adjacent territorial animals (Jennrich and Turner 1969). In order to estimate foraging habitat selection for either of the above scenarios, the null model must be subtracted or accounted for in the estimated UD (Fig. 1).

When modeling foraging-habitat selection for a central-place forager, failure to properly account for the central place in habitat-selection models will unintentionally lead to an estimation of the habitat around the central-place location, rather than foraging habitat. Although this may be important information, it is at a different scale than the question at hand. According to Johnson's (1980) scales of habitat selection, central-place selection would be second-order selection, while foraging-habitat selection would be third-order selection. Both are important to understand, but they are also different questions altogether.

Central-place foraging has been incorporated into some habitat selection models (Rosenberg and McKelvey 1999, Horne 2005, Rhodes et al. 2005). Rosenberg and McKelvey (1999) included distance to nest as an explanatory variable in their habitat-selection models. They demonstrated in simulations that failure to do so resulted in positive bias for habitats near central places. Since then, many resource-selection functions (Manly et al. 2002) have included distance to nest as a way of accounting for central-place-foraging behavior (e.g.,

Glenn et al. 2004). More recently Rhodes et al. (2005) included both distance to central place and distance from current location as variables in habitat selection models for koalas (*Phascolarctos cinereus*). Horne (2005) developed a modeling approach that simultaneously accounted for home range behavior, habitat selection, and interactions among individuals.

Recently Marzluff et al. (2004) and Millspaugh et al. (2006) suggested the use of utilization distributions (UDs) as an alternative measure of space use to resource-selection functions. Marzluff et al. (2004) developed a resource-utilization function (RUF) that related fixed-kernel UDs to resources on the ground to explain habitat selection by Stellar's jays (*Cyanocitta stelleri*) during the breeding season. Although Marzluff et al. (2004) accounted for autocorrelation in the UD, they did not explicitly account for central-place-foraging behavior. This may have biased their RUF to habitats near the nest site. The inclusion of a distance-to-nest term in their regression models would have accounted for the variability in space use associated with distance to the nest site. Millspaugh et al. (2006) champion the use of RUFs and provide several examples of RUFs, all of which assume uniform space use.

Many of the habitat-selection models mentioned previously provide a means to map the probability of an animal's habitat selection in a geographic information system (GIS). The ability to map preferred habitats should be an important factor in deciding how to model habitat selection. Maps can provide land managers with important information regarding an animal's predicted habitat and possible consequences of management decisions that might affect that habitat. Habitat-selection maps can be produced as long as the variables included in the models are available in a GIS. In the case of a central-place forager, this is not a problem as long as the central place is known. Habitat selection models containing a distance-to-nest variable usually use a GIS to calculate that variable, thus it would be

available to produce a map. However, only habitat that is associated with a particular central place can be mapped in this case. Most models are constructed using samples of known populations, not the entire population. Models can not be extrapolated to predict habitat for a population unless all central places are known. This puts habitat selection models that include a distance-to-nest term at a disadvantage over those that account for that behavior in another manner.

We extend the RUF method by Marzluff et al. (2004) to account for central-place foraging behavior in the northern goshawk (*Accipiter gentilis*). Goshawks are central-place foragers during the nesting season (Squires and Reynolds 1997). The male is the primary hunter during the incubation and early nestling stage. He returns from foraging trips either to the nest or to a nearby delivery site to provision the female and young (Reynolds et al. 1982). Some females begin hunting during the late-nestling stage, while others wait until young have fledged (Squires and Reynolds 1997). Male goshawks typically do not hunt near the nest during the breeding season (Ward and Kennedy 1994).

Greenwald et al. (2005) provided a review of goshawk habitat-selection studies in the western U.S. They reviewed all telemetry studies on goshawk habitat selection during the breeding season. Of 12 studies reviewed, 9 demonstrated selection for closed-canopy forests, large trees, and high-tree density. In addition, goshawks avoided large openings such as clearcuts and meadows. Interestingly, none of the researchers studied the influence of physical features of the landscape such as elevation, distance to streams, distance to roads, and topography, and none include a distance-to-nest variable in their models. These variables have been found to be important explanatory variables for other wide-ranging raptors such as California spotted owls (*Strix occidentalis occidentalis*; Irwin et al. 2007).

The objectives of this study were to: 1) develop a method to assess resource selection that is not biased toward the central place, and 2) develop a resource selection model that can be easily mapped in a geographic information system.

STUDY AREA

Our study took place within an 890,000-ha region of the Clearwater Mountains in northern Idaho, bounded in the south by the Middle Fork Clearwater River and in the north by the St. Joe River. Elevations ranged from 750-1500 m and annual precipitation ranges from 75-125 cm. Forests in this region are managed primarily for timber production, and the 3 primary landowners were Potlatch Forest Holdings, Inc., Idaho Department of Lands, and the U.S. Forest Service (Clearwater National Forest and Idaho Panhandle National Forest). Although forest types ranged from dry ponderosa pine (*Pinus ponderosa*) to cold subalpine fir (Abies lasiocarpa) habitat types, over 85% of the landscape consisted of mesic western redcedar (Thuja plicata) and western hemlock (Tsuga heterophylla) habitat types (Cooper et al. 1991). This landscape has a history of both natural and anthropogenic disturbance. Prior to European settlement, large stand-replacing fires occurred on the order of every 150-400 years within the western redcedar and western hemlock habitat types (Smith and Fischer 1997). Although fire suppression has reduced the frequency and extent of fires more recently, these lands are highly productive and intensive timber harvest has occurred in the region for the past 100 years. These disturbances have resulted in a heterogeneous forest structure, including early to late-seral stands.

Goshawk nesting habitat in our study area has been described by Hayward and Escano (1989). Goshawks usually nest in stick platforms built against the bole of live conifers below the canopy. Mean nest tree height is 31 m and dbh is 58 cm. Goshawks nest in

closed-canopy (75-85% overstory cover) conifer forests on moderate slopes. Goshawk nest stands have a mean basal area of 40 m^2 per ha. Highest tree densities per ha are comprised of the 7.6 to 17.8 cm dbh class (mean = 475), followed by the 17.8 to 30.4 cm dbh class (mean = 265), 30.4 to 60.9 cm dbh class (mean = 175), and trees >60.9 cm dbh (mean = 20). A summary of distances from goshawk nests to various habitat features is provided in Table 1.

METHODS

Telemetry

We randomly selected goshawks from 21 territories occupied in 2004-05. We captured adult goshawks in 2004-05 during the nestling stage of the breeding season using a great horned owl (*Bubo virginianus*) and dho-gaza nets (Bloom 1987). We attached 20-g and 30-g battery-powered satellite platform transmitter terminals (PTTs) to male and female goshawks, respectively, using backpack harnesses. All PTTs were manufactured by North Star Science and Technology and weighed <2.8% of body weight for males and <3.2% for females. Our PTTs were programmed to cycle on from 0700 to 1900 hr every other day during the breeding season (1 June – 31 August). We used location class 2 and 3 only because location class 1 and lower were considered too inaccurate for resource-selection studies (Moser and Garton 2007).

Utilization Distributions

We estimated individual 99% fixed-kernel UDs using telemetry locations from each goshawk using likelihood cross-validation (CV_h) to select the smoothing parameter (Horne and Garton 2006). Fixed kernels are non-parametric density estimators that result in a UD that is a continuous, probabilistic measure of space use (Worton 1989). Higher densities of telemetry points results in elevated values on the surface of a fixed-kernel UD, indicating

higher probabilities of space use. Conversely, low telemetry point densities results in lower values on the UD surface, indicating lower probabilities of space use (Fig. 1A).

We also estimated circular-normal UDs from these same telemetry locations (Fig. 1B). However, we set the nest location for each bird as the mean (x, y), which allowed us to objectively estimate the null space-use model for a central-place forager. We used the program developed by Horne (2005) to calculate the circular-normal UD, and we set the extent of the circular-normal UD to the extent of the 99% fixed-kernel UD.

We calculated a bias-corrected UD by subtracting the circular-normal UD from the fixed-kernel UD at each cell location (Fig. 1C). This resulted in a new UD surface with a range of individual probabilities: negative values indicating habitat avoidance and positive values indicating selection. We performed a percent rank function in Excel (Microsoft Corporation, Redmond, Washington) on the values to standardize them similar to Marzluff et al. (2004), resulting in a range of values from 0 to 1 that corresponded to a relative probability.

Spatial Layers

We used a GIS to combine values of our uncorrected fixed-kernel and bias-corrected UDs with potential explanatory variables. We used Landsat 7 imagery from 2004 and 2005 to create 3 cover types varying in tree dbh and canopy closure (Table 2). We ground-truthed all nest areas to determine cover-type classification accuracy by systematically placing 48 plots and measuring trees per ha on variable radius plots using a 20-BAF factor and a densiometer to measure overstory tree canopy closure. Plots were systematically arranged in a radiating fashion from the nest tree. Classification accuracy for high-canopy closure was

92% for 2004 and 87% for 2005, for moderate-canopy closure 78% in 2004 and 75% in 2005, and for openings 89% in 2004 and 94% in 2005.

We also included physical environmental data layers such as 2nd order and larger streams, primary, secondary, and tertiary roads, elevation, and ridgetops (Table 2). We used the "distance to" command in ArcGIS 9.0 to create raster layers for each of the above data layers. We used a distance-based approach rather than discrete categories because distance-based approaches are less prone to misclassification of habitat use due to telemetry error (Conner et al. 2003). In addition, distance-based analyses can provide more information on habitat selection than classification-based approaches such as use of edges between cover types (Conner et al. 2003). We converted all data layers to rasters and then combined them to provide a database relating each goshawk's uncorrected and bias-corrected UD to the possible explanatory variables.

Modeling

We estimated bias-corrected and uncorrected RUFs for pooled male goshawks and pooled female goshawks using regression trees in CART 6.0 (Salford Systems, San Diego, California). Regression trees are a non-parametric modeling technique used to explain the variation of a single response variable using multiple explanatory variables (Breiman et al. 1984). The main purpose of a regression tree is to produce a tree-structured prediction rule to explain the relationships that exist between the response and explanatory variables. Regression trees identify complex hierarchical relationships in multivariate data by repeatedly splitting the data into increasingly smaller subsets in an attempt to minimize the variance in each subset. The model is initially over fit, and the resulting tree is pruned using

10-fold cross-validation to select the most parsimonious model that best explains the relationship between the explanatory and response variables (Breiman et al. 1984).

Regression trees have been used in numerous ecological studies and often outperform linear models (De'ath and Fabricius 2000). Regression trees are often able to elucidate complex relationships among explanatory variables that would be otherwise difficult to specify in linear models (e.g., Andersen et al. 2000). Furthermore because they are non-parametric they do not need to meet many of the assumptions required of parametric techniques such as linear models. Regression trees are also relatively robust to autocorrelation (Cablk et al. 2002, Segurado et al. 2006), an issue identified by Marzluff et al. (2004) when they developed RUFs for Stellar's jays.

We developed both uncorrected and bias-corrected RUFs for both male and female goshawks. Furthermore, we developed 2 types of models for each corrected and uncorrected RUF, one incorporating a distance-to-nest variable (Table 2) and one without. This allowed us to compare the effects of including a distance-to-nest term in both uncorrected and corrected models. Model fit was evaluated based on relative error, which is the mean square error of the resulting model divided by the variance in the entire data set. The relative error provides a metric to judge model fit in relation to the variance in the data (Breiman et al. 1984). Although multiple competing models may result from regression tree analyses, we reported only the best model for each response variable. Regression trees also provide a measure of the relative importance of each explanatory variable in the model, called variable importance. Variable importance is the relative contribution of each explanatory variable in explaining the variation in the final model (Breiman et al. 1984). Comparing variable

importance values in a regression tree is analogous to comparing relative coefficient values in a linear model when those values have been standardized.

We assumed that most space use away from the nest during the breeding season is due to foraging behavior. However, goshawks are territorial and some of this space use may be defensive behavior, or other types of interactions with con- or hetero-specifics. Therefore, we refer to our models as depicting foraging habitat when in fact they predict space use for a variety of behaviors.

RESULTS

We captured and radio tagged 7 male and 12 female goshawks from 14 nest sites. Mean (SE) number of telemetry locations was 61 (22) for males and 80 (49) for females.

Male Goshawks

Uncorrected RUFs identified distance to nest as clearly the most important variable in the model, followed by elevation and distance to opening (Table 3). The influence of distance to nest in uncorrected RUFs had a masking effect on other variables in the model as suggested by the large difference in variable importance values. The model predicted the highest probability of space use when distance to nest ≤1854 m. The model predicted lowest probability of space use when distance to nest was >3009 m (Fig. 2).

Uncorrected RUFs that excluded distance to nest as a potential explanatory variable identified elevation and distance to opening as the most important variables predicting goshawk space use (Table 3). The model predicted the highest probability of space use when distance to opening was \leq 232 m and elevation was 844 to 1113 m. The model predicted lowest probability of space use when elevation was \leq 844 m and \geq 1113 m (Fig. 3).

Corrected RUFs that excluded distance to nest identified distance to stream as the most important variable in the model, followed by elevation and distance to ridge (Table 3). The model predicted the highest probabilities of space use when distance to stream ≤1009 m, elevation was 889 to 1045 m, and distance to ridge >120 m. The model predicted the lowest probabilities of space use when elevation >1020 m and distance to stream >1009 m (Fig. 4).

Corrected RUFs that included distance to nest identified distance to nest as the most important variable in the model, followed by elevation and distance to stream (Table 3). The model predicted highest probabilities of space use when distance to stream \leq 1009 m, elevation \leq 1045 m, and distance to nest \leq 1707 m. The model predicted the lowest probabilities of space use when distance to stream >1009 m and distance to nest \leq 2624 m (Fig. 5)

Female Goshawks

Uncorrected RUFs selected distance to nest as clearly the most important variable in the model, followed by elevation, distance to opening, distance to stream, distance to high canopy closure, and distance to road (Table 4). Once again the influence of distance to nest in uncorrected RUFs had a masking effect on other variables in the model as suggested by the large differences in variable importance values. The model predicted the highest probabilities of space use when distance to nest \leq 904 m and distance to high canopy closure \leq 181 m. The model predicted the lowest probabilities of space use when distance to opening <184 m, distance to stream \leq 1316 m, distance to nest 1332 to 2742 m, elevation 847 to 1092 m, and distance to road >192 m (Fig. 6).

The uncorrected RUF that excluded distance to nest as a potential explanatory variable identified distance to opening, elevation, distance to stream, distance to road, and

distance to high canopy closure as the most important variables in the model (Table 4). The model predicted the highest probabilities of space use when distance to opening >184 m and elevations were 880 to 1063 m. The model predicted the lowest probabilities of space use when distance to opening <184 m, elevation <1092 m, distance to high canopy closure >22 m, and distance to stream ≤1316 m (Fig. 7).

Corrected RUFs that excluded distance to nest identified elevation as the most important variable in the model, followed by distance to opening, distance to road, distance to moderate canopy cover, and distance to stream (Table 4). The model predicted the highest probabilities of space use when elevation \leq 1052 m and distance to opening \geq 228 m and distance to road \geq 171 m. The model predicted the lowest probabilities of space use when elevation \leq 1052 m, distance to opening \leq 228 m, and elevation \leq 866 m (Fig. 8).

Corrected RUFs that included distance to nest identified distance to nest as the most important variable in the model, followed by elevation, distance to opening, and distance to stream (Table 4). The model predicted the highest probabilities of space use when distance to nest >3671 m and distance to stream >521 m. The model predicted the lowest probabilities of space use when distance to nest \leq 3671 m, distance to opening \leq 70 m, and elevation \leq 866m (Fig. 9).

Relative errors were lowest for uncorrected RUFs that included a distance-to-nest term (Table 3, 4). Bias-corrected models for male goshawks were improved by including distance to nest as a potential explanatory variable, but not for models for female goshawks (Table 3, 4). The inclusion of distance to nest in the bias-corrected models for male goshawks improved the relative error without masking the importance of other variables as evidenced by the variable importance weighting (Table 3).

DISCUSSION

Bias-corrected RUFs reveal goshawk selection for habitat features not evident in uncorrected RUFs. Regression trees select only the variables that contribute the most to explaining the variation in the data. In the uncorrected RUFs, distance to nest was selected as the most important variable at the cost of excluding other variables that may have been important. Although including distance to nest as a variable in a linear model would allow for the effects of this variable while simultaneously assessing the contributions of other variables, the disadvantages to this approach would be the potential difficulty in specifying some of the complex interactions that the regression trees unveiled, as well as potential influence of spatial autocorrelation on variable selection procedures (Segurado et al. 2006). Autocorrelation in linear models may result in smaller variance terms for explanatory variables, resulting in selection for these variables in the model when in fact they may not be statistically significant predictors.

All of the models included elevation as either the first or second most important variable. We found that male goshawks appear to be using habitats along lower slope positions near streams. A number of other studies have documented use of closed canopy forests with larger trees (Bright-Smith and Mannan 1994, Greenwald et al. 2005), and others have suggested use of edges within these forests (Kenward 1982). However, to our knowledge no other studies have identified topographic features such as lower slope positions near streams as important goshawk habitat. Riparian zones are productive areas relative to uplands and one would expect higher densities and diversity of prey (Thomas 1979) which may attract foraging goshawks.

Female goshawks appear to be more sensitive to the complex interactions between elevation, proximity to openings, roads, and streams. They seemed to use lower elevations as long as these areas were away from openings and roads. In contrast, they selected areas of higher elevation that were somewhat closer to openings. They avoided low elevations near openings that were away from streams and roads. Again, our study may be the first to report the importance of non-vegetative variables for female goshawk habitat; although Hargis et al. (1994) reported some goshawks used areas near water sources. Our results are similar to those of Hargis et al. (1994) and Sonsthagen et al. (2006) who reported most female goshawks in their study used forested habitat in greater proportions than forest openings or nonforest.

No other studies of goshawk habitat selection have included distance to nest as a variable in the final model, so those studies may be biased towards habitat near the nest site. It would be difficult in many cases to recognize this problem, because the vegetative components of goshawk nesting habitat may in fact be similar to those of foraging habitat. Thus, many resource-selection studies may be identifying the wrong foraging habitat. Rather, these studies may indeed be estimating 2nd order resource selection rather than 3rd order resource selection (Johnson 1980).

Although our bias-corrected RUFs provided insights into the space use behavior of goshawks, our models also contained a large amount of relative error. The relative error statistic in regression trees is analogous to $1 - r^2$ in a multiple regression analysis. Our corrected models without the distance-to-nest term explained approximately 17% of the variation in the data. However, when we included distance to nest in our bias-corrected models for male goshawks, the amount of variation explained improved to 30% indicating

we were not able to completely remove the effect of distance to nest in our bias-corrected UDs. High error in our models suggested there may be additional factors affecting goshawk space use in our study. Furthermore, variability among individuals in their selection of habitat was not accounted for, which added to the variability in the final models. In addition, the use of UDs as the response variable may add further noise to the data, particularly when using a smoothing factor such as CV_h . Horne and Garton (2006) demonstrated that CV_h results in more smoothing in the UD than least-squares cross-validation (LSCV_h). Extra smoothing would result in more difficulty defining sharp boundaries of fine-scale selection by goshawks, such as use of small patches. We attempted to alleviate this issue by using distance-based analyses, but this did not completely resolve the issue. Perhaps use of LSCV_h or using a proportion of the recommended CV_h (e.g., 80%) would help alleviate this issue.

Although we used regression trees to model the relationship between explanatory variables and UD probabilities, a variety of other modeling approaches are available for this type of analysis (Millspaugh et al. 2006). Both Horne (2005) and Rhodes et al. (2005) used linear models in resource selection approaches. Although the resulting models are more elegant than ours, we think our approach is intuitive and is also flexible as to the type of modeling approach that can be used. We believe regression trees have some advantages over linear models such as not having to meet assumptions required for parametric models, robustness to autocorrelation, and ability to easily model high-order interactions. However, disadvantages include the inability to average individual models. Indeed Marzluff et al. (2004) touted the use of RUFs over traditional RSFs and other resource selection models due to the ability to model habitat selection of individuals, which is more appropriate than pooling the data from all of the individuals.

We believe that the use of RUFs has utility in resource selection studies. Furthermore, we think that studies of central-place foragers may benefit from using a bias-corrected RUF approach. Much like Marzluff et al. (2004) regarding the use of RUFs, our approach of using bias-corrected RUFs may be most beneficial as a technique to build and improve upon by other researchers.

Our study was limited by small sample sizes, particularly for male goshawks.

Furthermore, high variability, particularly for female goshawks resulted in models that were complex and did not explain much of the variation in the data. Our study was also of a relatively short duration. Future studies would benefit from extending the study period in order to account for temporal variation in prey densities and weather patterns, which may affect foraging behavior.

MANAGEMENT IMPLICATIONS

Bias-corrected RUFs can elucidate important habitat relationships that otherwise may be masked by the influence of distance to the central place. Furthermore, because bias-corrected RUFs remove this influence rather than include it in the model, the predicted probabilities of space use can be mapped for the entire population without having to know the location of each central place. Models developed from the sample can be extrapolated to the entire population assuming samples are random and representative of the population of interest.

Goshawk foraging habitat may include more nonvegetative variables than other studies have reported, particularly elevation. Habitats near streams may also be more important as male goshawk foraging habitat than previously thought. Because male goshawks are the primary provider during the nesting season (Younk and Bechard 1994,

Squires and Reynolds 1997), managers should consider these habitats to be important for the conservation of goshawks during the nesting season.

Our models are specific to goshawks in northern Idaho and we caution against applying these models directly to other populations. However, the patterns of habitat use uncovered by these models may be useful to other researchers when designing studies to assess habitat selection for other goshawk populations.

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Table 1. Habitat variables associated with nest sites (n = 14) from which adult goshawks were captured and fitted with satellite transmitters for use in habitat selection analyses, Idaho, 2004-2005.

Variable	Mean (SD)	
Distance (m) to		
Stream	463 (322)	
Road	117 (104)	
Ridge	103 (56)	
High canopy cover	0 (0)	
Moderate canopy cover	95 (76)	
Opening	179 (87)	
Elevation (m)	1010 (125)	

Table 2. Explanatory variables included in regression tree analyses of goshawk habitat selection, Idaho, 2004-2005.

Variable	Description
Distance to nest	Euclidean distance (m) to nest tree occupied in current year
Elevation	Elevation (m) above sea level
Distance to stream	Euclidean distance (m) to nearest 2 nd order or higher stream
Distance to ridge	Euclidean distance (m) to nearest ridge top
Distance to road	Euclidean distance (m) to nearest primary, secondary or
	tertiary road
Distance to high canopy	Euclidean distance (m) to nearest patch containing overstory
	trees with >70% canopy cover and dbh >31 cm
Distance to mod canopy	Euclidean distance (m) to nearest patch containing overstory
	trees with 30-69% canopy closure and dbh 13-30 cm
Distance to opening	Euclidean distance (m) to nearest patch containing trees with
	<30% canopy closure and dbh <13 cm. Includes meadows and
	agriculture

Table 3. Relative importance of habitat variables and relative error of regression tree models for male goshawks, Idaho, 2004-2005.

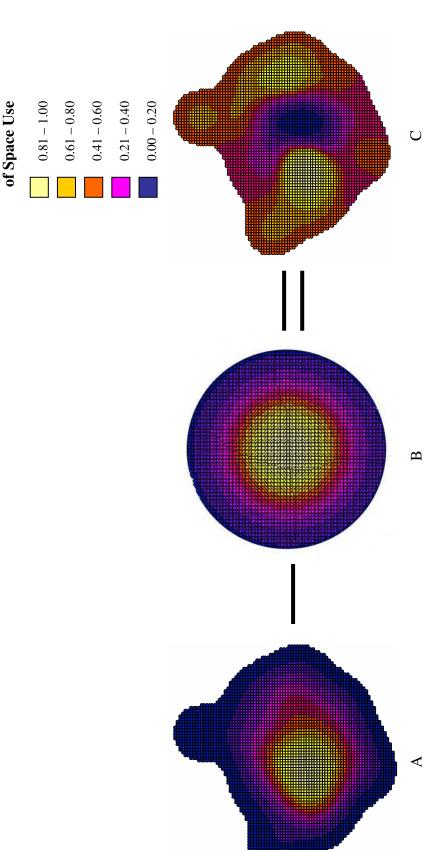
Model	Variable	Relative Importance	Relative Error
Uncorrected with distance to nest	Distance to nest Elevation	100	0.53
Uncorrected without distance to nest	Elevation Distance to opening	100	0.93
Corrected without distance to nest	Distance to stream Elevation	100	0.83
Corrected with distance to nest	Distance to ridge Distance to nest Elevation	13 100 55	0.71
	Distance to stream	50	

Table 4. Relative importance of habitat variables and relative error of regression tree models for female goshawks, Idaho, 2004-2005.

Model	Variable	Relative Importance	Relative Error
Uncorrected with distance to nest	Distance to nest	100	0.67
	Elevation	23	
	Distance to opening	12	
	Distance to stream	7	
	Distance to high canopy	7	
	Distance to road	3	
Uncorrected without distance to nest	Distance to opening	100	0.89
	Elevation	71	
	Distance to stream	44	
	Distance to road	16	
	Distance to high canopy	14	

Corrected without distance to nest	Elevation	100	0.83
	Distance to opening	77	
	Distance to road	22	
	Distance to moderate canopy	7	
	Distance to stream	9	
Corrected with distance to nest	Distance to nest	100	0.86
	Elevation	38	
	Distance to opening	31	
	Distance to stream	21	

Relative Probability



site for Fig. 1A and 1B. Central-place foraging behavior is accounted for by subtracting the cell probabilities in Fig. 1B from utilization distribution, and (C) 99% bias-corrected utilization distribution. The highest probabilities of use are near the nest Figure 1. Space use of a male goshawk depicted by: (A) 99% fixed-kernel utilization distribution, (B) 99% circular-normal those in Fig. 1A, resulting in a bias-corrected utilization distribution that indicates habitat selection away from the nest.

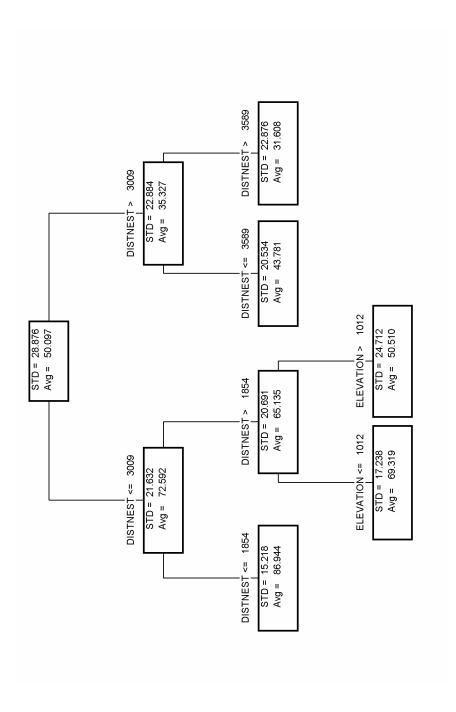


Figure 2. Uncorrected habitat selection model for male goshawks including distance to nest as a potential explanatory variable. Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

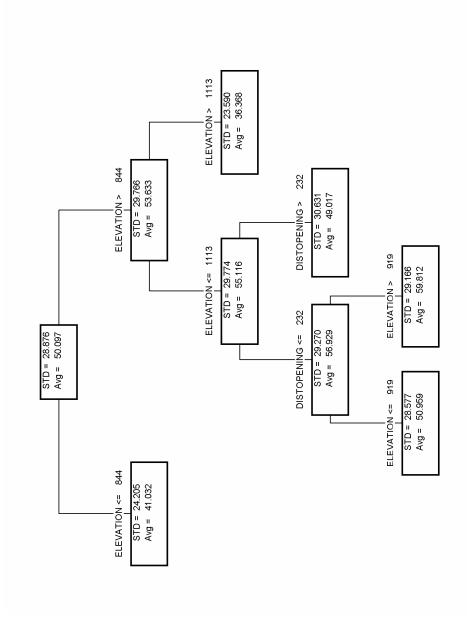


Figure 3. Uncorrected habitat selection model for male goshawks excluding distance to nest as a potential explanatory variable. Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

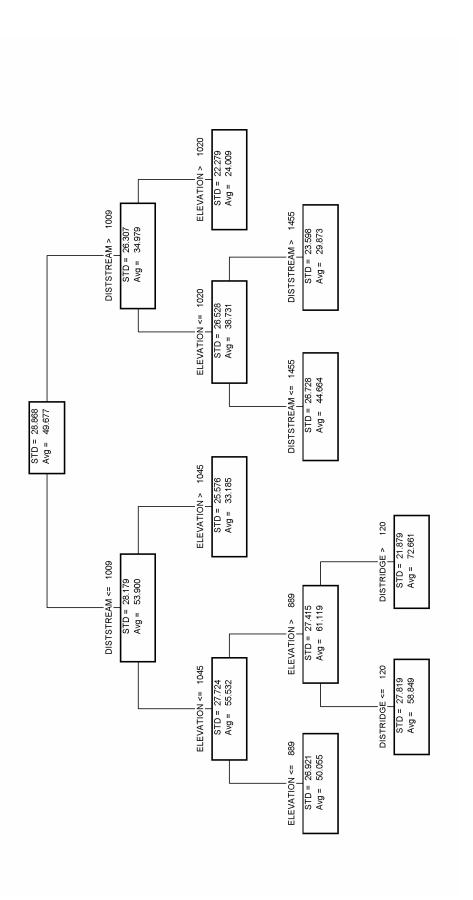


Figure 4. Corrected habitat selection model for male goshawks excluding distance to nest as a potential explanatory variable. Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

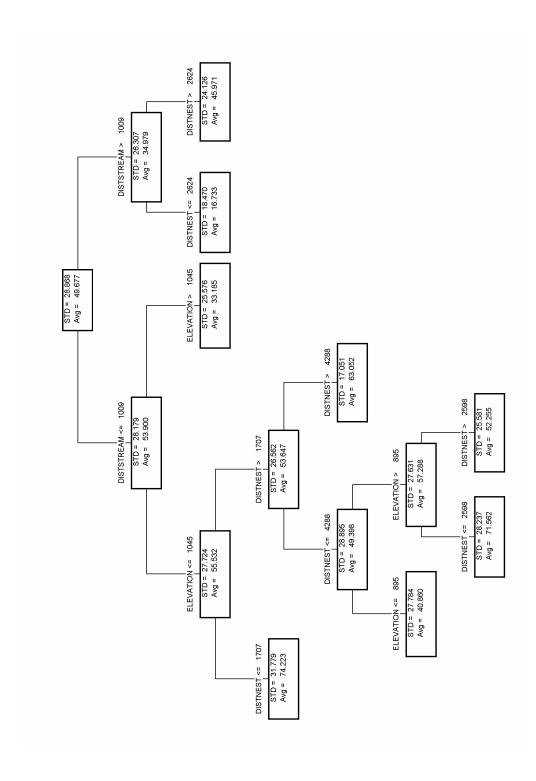


Figure 5. Corrected habitat selection model for male goshawks including distance to nest as a potential explanatory variable. Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

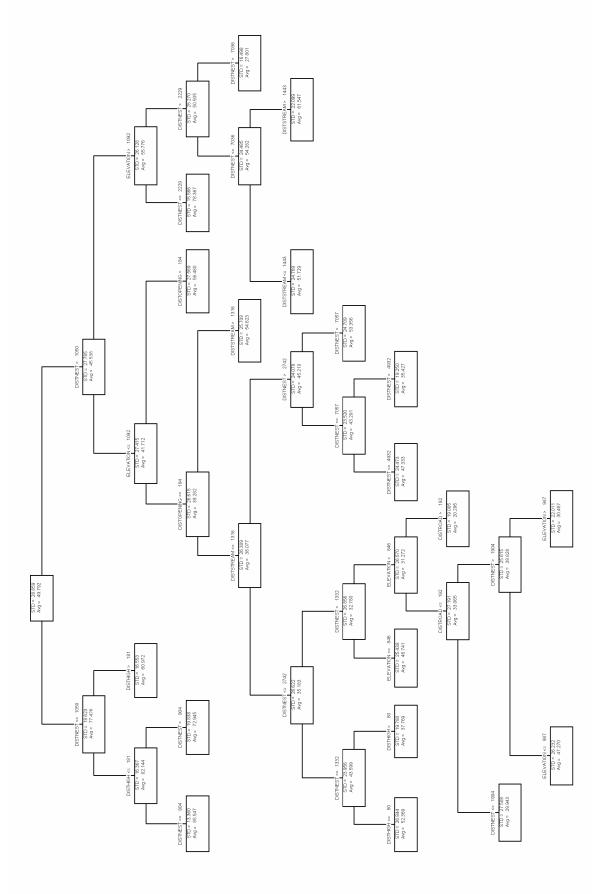


Figure 6. Uncorrected habitat selection model for female goshawks including distance to nest as a potential explanatory variable.

Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

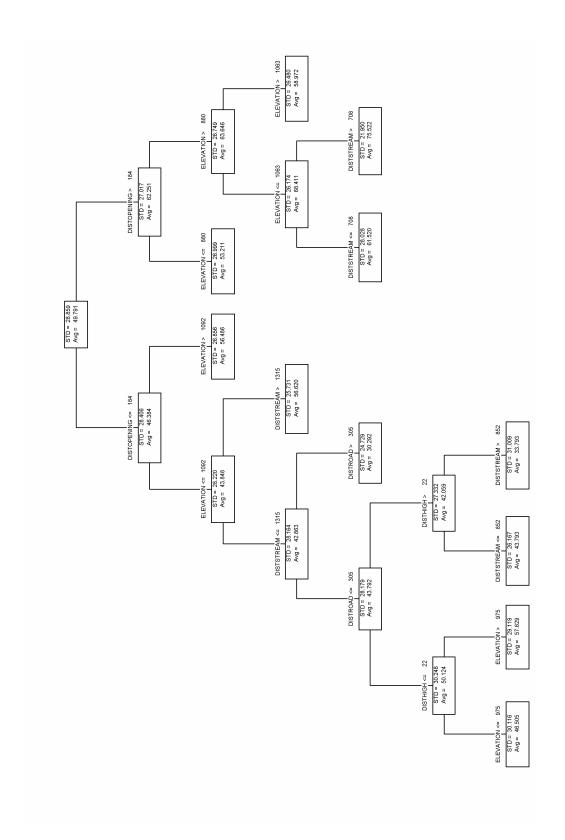


Figure 7. Uncorrected habitat selection model for female goshawks excluding distance to nest as a potential explanatory variable.

Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

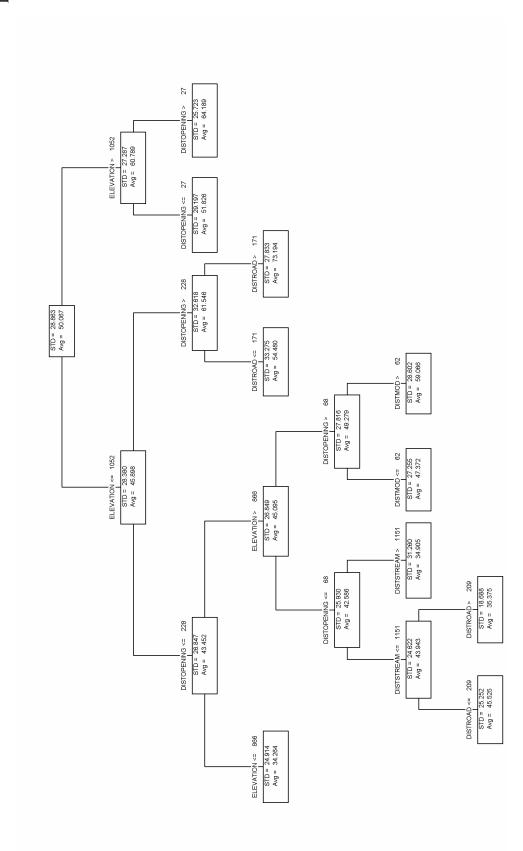


Figure 8. Corrected habitat selection model for female goshawks excluding distance to nest as a potential explanatory variable. Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

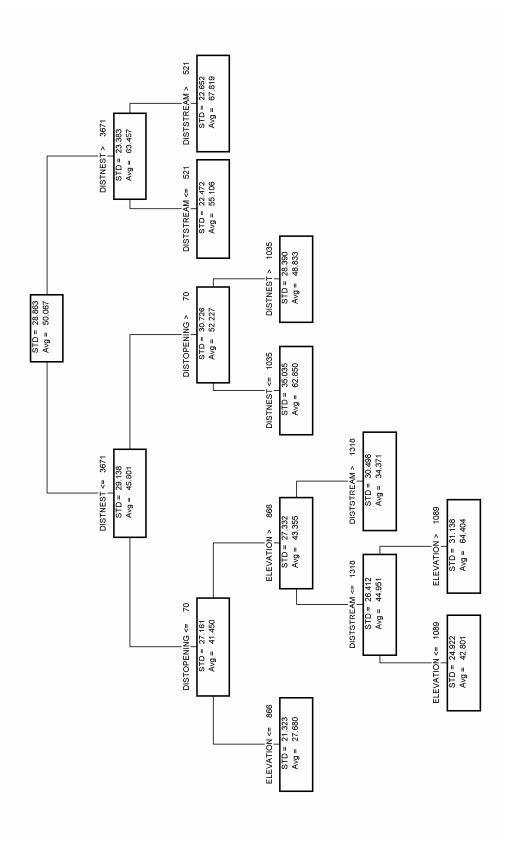


Figure 9. Corrected habitat selection model for female goshawks including distance to nest as a potential explanatory variable. Values in each node are the mean (SD) relative probabilities of space use associated with each decision rule.

Chapter 6. Conclusion

It is likely that a number of factors interact to affect goshawk reproduction in northern Idaho, including habitat conditions (Crocker-Bedford 1990), weather (Fairhurst and Bechard 2005), prey availability (Salafsky et al. 2005), competition (Kostrzewa 1991), predation (Boal and Mannan 1994), siblicide (Boal and Bacorn 1994), and parasitism (Cooper and Petty 1988). The interactions of these factors may be complex and it may be difficult to fully understand their effects. However, habitat may be a primary factor that can exert influence on some of the others such as prey availability (Drennan and Beier 2003), competition (LaSorte et al. 2004), and predation (Manolis et al. 2000). Although my study was of short duration, I was able to demonstrate that within 2 years following habitat modification by timber harvesting goshawk territory reoccupancy was not affected until <39% of the 170-ha territory was left in suitable nesting habitat. Furthermore, timber harvesting did not appear to have an effect on nesting success during that time period. What is unknown is whether there will be delayed responses in prey availability, competition, or predation as a result of habitat modification. Winter and spring weather appeared to have a strong influence on nesting success. Global climate change will likely continue to influence weather patterns, and thus will have either a negative or positive effect on goshawk reproduction depending on the locale.

I found that female goshawks are residents in this area, and that both male and female goshawks have relatively large home ranges that are a function of nesting success and the proportions of openings and closed-canopy forest within their home range. I also demonstrated that in addition to vegetative features, goshawks often select habitats within their home ranges based on geophysical attributes such as elevation, distance to stream, and

distance to ridges. These features have historically not been considered in goshawk management plans (e.g., Reynolds et al. 1992).

MANAGEMENT IMPLICATIONS

Timber harvest can be conducted within goshawk home ranges and even 170-ha territories around the nest site without adverse impacts as long as appropriate amounts of suitable habitat are retained. We defined suitable habitat for nesting and habitat within the home range presumably for foraging as stands with overstory trees >70% canopy cover and >31 cm dbh. Although classification trees suggested a threshold of 39% suitable habitat within the territory should be retained in order to ensure goshawk reoccupancy, I recommend leaving ≥50% when possible to increase the probability of reoccupancy. This would also help address the uncertainty surrounding long-term effects of habitat modification on competition or predation. It may even be possible to create suitable goshawk habitat through timber harvest by doing a commercial thinning, which removes understory trees and leaves much of the overstory (Reynolds et al. 1992, McGrath et al. 2003). I did not address patch size in this study, but preliminary data indicate goshawks may prefer to nest in larger nest stands (>50 ha) with more interior habitat than randomly available stands.

Male goshawk home range sizes were sensitive to the proportion of openings within the home range. For example, when all other factors are held constant, my model estimates a male goshawk home range size to increase by 43% if the proportion of openings increases from 20% to 40%. The need to traverse larger home ranges is likely to have energetic costs that may affect individual fitness. Thus, managers should attempt to balance forest structure at a landscape level to provide reasonable proportions of openings, moderately closed-canopy forest, and high closed-canopy forest. Although I did not identify a threshold, it seems

reasonable to maintain landscapes in >40% high closed-canopy forest, <30% in openings or young forest, and 30% in moderately closed-canopy forest. These recommendations are similar to those of Reynolds et al. (1992) and would also provide the minimum amount of suitable habitat necessary to maintain occupancy of goshawk nesting territories. Furthermore, because male goshawks, the primary food provisioner during the nest season, select habitats between 889 to 1045 m, and within 1009 m of streams, closed-canopy forests with these attributes should be a higher priority for retention on the landscape than closed-canopy forests at other elevations or further from streams.

RESEARCH IMPLICATIONS

Much work remains to be done with regards to the effects of timber harvesting on goshawk reproduction. Longer-duration studies with larger sample sizes are needed to better understand the consequences of habitat modification within goshawk territories. These studies would also benefit from multiple study sites in different forest types, particularly those differing in productivity so that the productivity hypothesis can be tested (Huston 1994). If possible, birds should be radio marked to better understand individual turnover rates among territories. Long-term studies incorporating other factors such as weather, prey availability, competition, and predation could help unravel these potentially interacting factors.

Habitat-selection studies should be conducted at multiple scales to better understand processes affecting goshawk habitat selection. Future research should examine configuration of habitats within home range boundaries, or Johnson's (1980) 2nd order habitat selection. Furthermore, little is known about goshawk winter habitat selection. Future studies are needed to better understand which habitats are important for goshawks wintering in this

region. Long-duration radio-telemetry studies could also shed some light on the frequency that migration may occur due to fluctuations in resources during the winter.

Techniques to better characterize goshawk habitat from remotely-sensed data would be very useful for habitat-selection studies. Lidar has the potential to provide more biologically-relevant habitat information than data derived from Landsat imagery, which provides cover types that are merely a surrogate for forest structure (Hyde et al. 2006). Lidar can provide information regarding both overstory and understory structure, as well as accurate elevation models. These data could be used to develop more accurate habitat selection models for goshawks.

A variety of modeling approaches are available to characterize goshawk habitat selection. Different approaches could be used to see which one(s) best characterize goshawk habitat. Future work based on utilization distributions should test the sensitivity of different bandwidth-selection procedures to see how bandwidth selection affects the ability of models to identify important habitat features for goshawks.

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